

STINGLESS BEES (MELIPONIDAE)
OF THE
WESTERN HEMISPHERE

HERBERT F. SCHWARZ

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¹ Died August 25, 1947.

STINGLESS BEES (MELIPONIDAE) OF THE WESTERN HEMISPHERE

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LESTRIMELITTA *AND THE FOLLOWING SUBGENERA OF*
TRIGONA: TRIGONA, PARATRIGONA, SCHWARZIANA,
PARAPARTAMONA, CEPHALOTRIGONA, OXYTRI-
GONA, SCAURA, *AND MOURELLA*

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WITH A BIBLIOGRAPHY BY HERBERT F. SCHWARZ
AND ANNETTE L. BACON

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PREFACE

A NUMBER OF YEARS AGO (1932a) I published a paper on the stingless bee genus *Melipona* of the New World. At the time it was my hope to follow this after a short interval with an account of the New World species of the closely related genus *Trigona*, but while several shorter papers dealing regionally with this genus have been issued, including some papers devoted to Old World forms, I have had to defer until now the publication of a report of more embracing scope. Even so, the present work is only a substantial fragment rather than a completed whole. Certain of the subgenera of *Trigona* still require study before they are in readiness for issue. It seemed, however, of service to issue now the subgenera that had been completed rather than to wait until the several uncompleted subgenera could also be included. The groups here considered are *Lestrimelitta* and the following subgenera of *Trigona*: *Trigona*, *Paratrigona*, *Schwarziana*, *Parapartamona*, *Cephalotrigona*, *Oxytrigona*, *Scaura*, and *Mourella*. Subgenera on which work is still in progress but which, it is hoped, will be published ultimately as a supplement to the present work include: *Hypotrigona*, *Partamona*, *Tetragona*, *Plebeia*, *Nannotrigona*, and *Scaptotrigona*.

Although these uncompleted subgenera are excluded from the body of the text, there are allusions to them throughout the Introduction. This seeming inconsistency has its justification in the fact that there are so many suggestive resemblances in the biology of the stingless bees from group to group that an enlightening picture of their ways can hardly be obtained without including the known facts regarding the family as a whole. For this reason I have been impelled in the Introduction to draw upon the bibliography of the Old World species as well as the New, hoping thereby to give a somewhat more precise picture of the place of the stingless bees in the scheme of things.

The scope of the Bibliography will indicate how many writers have found these bees of engrossing interest or at least worthy of comment. Nevertheless, after sifting the recorded statements and fitting the observations into the framework of the whole, one

can but wonder at the paucity of our present knowledge regarding these insects. More than 150 years have gone by since the first meliponid was described, and yet there are many fundamental facts regarding the ways of life of these bees that have eluded successive investigators, while in other instances the evidence gathered by one observer is at variance with that obtained by another, making for caution in drawing categorical conclusions.

One could, however, hardly expect a different status of things. There is no insect that has aroused such universal interest as the honeybee. It has been "voluminously discussed"—to adopt the expressive phrase of Phillips (1928, p. 456)—in thousands of books and magazine articles, the mere listing of which would exhaust the space of an average book. Years ago the bibliography of bee-keeping compiled by the Bureau of Entomology contained not far from 30,000 titles and it is probably substantially larger today. Does that mean we know everything there is to be known regarding the honeybee? Far from it. The comparatively recent discoveries of von Frisch, including what has been referred to—a little sensationally—as "the language of the bees," is proof how rewarding may be investigations even on this much studied insect.

Yet the honeybee (*Apis mellifera* Linnaeus) represents but one species, albeit many varieties, while the meliponids consist of a vast and complicated aggregate. Also the honeybee today is to be found the world over wherever civilization has stretched and flowers are available, and it is largely a domestic insect. The stingless bees, on the other hand, are confined to the tropics or at most reach the subtropics here and there and, being largely a forest fauna, are often not readily accessible for observation even within their restricted domain. The material assembled in the Introduction is no more, therefore, than a suggestion of the picture as a whole. It may be compared perhaps to the fragmentary assemblage of a few related parts in a jigsaw puzzle. These parts give hints of the complete composition but leave also great gaps to be filled. If what is set down in the

Introduction, supplemented by the additional facts that appear in the discussions of the several species, prompts others to study the

ways of these bees in greater detail, one of the objectives of this publication will have been achieved.

ACKNOWLEDGMENTS

It is no easy task to search one's memory for the many who have given aid in the preparation of a monograph like the present one, which has been carried on intermittently over a stretch of years, and I am very conscious how indispensable has been this friendly assistance. The present work might never have been undertaken except for the encouragement of the late Dr. Frank E. Lutz, of the American Museum of Natural History, who himself had found the stingless bees of exceptional interest and characteristically wished others to share in a field he had found attractive and rewarding. I have relied on his judgment throughout.

Without the kind cooperation on the part of a number of scientific institutions the specimens on which this work is so largely based would not have been available, but even more than for the original loans of material do I feel indebted to these institutions for their great patience in extending the loans so that the investigation might be continued. I am under heavy obligations among others to the following for placing at my disposal their collections of unidentified Meliponidae: Academy of Natural Sciences of Philadelphia, British Museum (Natural History), Cornell University, Museum of Comparative Zoölogy, University of Michigan, and United States National Museum. These collections, taken in conjunction with those in the American Museum of Natural History, have been of great aid.

The loan of material by the British Museum (Natural History) included some specimens acquired from Mrs. Farren White that were originally in the Frederick Smith collection as well as a goodly number bearing the label of the Godman-Salvin collection. Among the individual collectors represented in this loan appear such names as G. E. Bodkin, H. E. Box, C. J. Brooks, G. E. Bryant, G. C. Champion, L. E. Cheesman, Churchill, E. B. Cornell, M. T. Daws, A. Ducke, F. and M. Edwards, Forrer, F. D. Godman, G.

Hammond, M. D. Haviland, K. J. Hayward, Janson, G. B. Longstaff, S. Moore, V. Patten, B. Piffard, A. H. Ritchie, J. Rodway, H. Rogers, H. B. Smart, H. H. Smith, D. Swainson, A. K. Totten, and C. B. Williams. To the British Museum I am indebted, too, for the opportunity of examining the specimens collected by the expedition of Oxford University to British Guiana in 1929.

Among the specimens made available by the United States National Museum first place should be given to the stingless bees obtained by Dr. W. M. Mann in Bolivia while on the Mulford Expedition of 1921-1922, but a number of other collectors contributed also to the aggregate. Mention should be made in this connection of J. M. Aldrich, H. W. Atkinson, C. F. Baker, H. S. Barber, S. F. Blake, A. Busck, M. A. Carriker, W. P. Cockerell, J. C. Crawford, C. C. Deam, F. J. Dyer, K. Fiebrig, G. P. Goll, L. O. Howard, A. H. Jennings, F. Knab, H. F. Loomis, M. W. Lyon, Jr., R. E. B. McKenney, Miss H. B. Merrill, A. W. Morrill, Herbert Osborn, A. Reyné, W. Robinson, G. P. Russell, H. Sargent, E. A. Schwarz, C. H. T. Townsend, and J. Zetek.

The Department of Entomology of Cornell University submitted the stingless bees obtained on successive expeditions made by members of its staff to South America. The expedition of 1919-1920 worked on the west coast of that continent and in Brazil. Participants in this expedition were Prof. J. C. Bradley and Dr. W. T. M. Forbes, who were accompanied part of the time by R. G. Harris and J. H. Williamson. The expedition of 1927 to Surinam had as participants Dr. Forbes and Dr. P. P. Babiş. Specimens obtained by Professor Bradley in Central America were also included in the loan, as were those of J. C. Crawford (C. F. Baker collection) and of A. G. Hammar. What has further enhanced the value of the material sent me from Cornell University is the inclusion of specimens identified by both A.

Ducke and by C. Schrottky, thus clarifying doubts that might have existed regarding the interpretations of these two students of the Meliponidae.

The specimens lent by the Academy of Natural Sciences of Philadelphia consist in part of those that were collected many years ago by H. H. Smith, but in addition there are a number taken by S. Brown, G. B. Fox, D. E. Harrower, W. Huber, C. H. Lankester, J. F. McClendon, and J. A. G. Rehn.

The names of F. M. Gaige and T. H. Hubbell predominate on the specimens lent by the University of Michigan.

Among those whose names appear as collectors of the specimens kindly submitted by the Museum of Comparative Zoölogy at Harvard University are A. Agassiz, A. Alfaro, N. Banks, T. Barbour, M. Bates, José Blaser, W. S. Brooks, Wm. Clarke-MacIntyre, J. C. Crawford, P. J. Darlington, Jr., J. B. Edwards, Kellerman, J. Ogilvie, Pommerat, J. B. Smith, R. E. Stadelmann, Father Stanton, N. A. Weber, D. Wees, and W. M. Wheeler.

Loans made by scientific institutions are rivaled in range and interest of specimens by the material made available through certain individuals. I am under lasting obligations for the large collections from Costa Rica donated by Dr. Anastasio Alfaro and also by Mr. Ferd. Nevermann, in both cases accompanied by valued field notes and much stimulating correspondence.

Dr. William Beebe's material from British Guiana included not only his own collecting but sizable series taken by A. E. Emerson, J. F. W. Pearson, J. Tee-Van, R. E. Wheeler, W. M. Wheeler, and others. The British Guianan specimens received were supplemented by other specimens from the same country that had been collected by Mr. and Mrs. J. Ogilvie and by Miss A. Mackie and that were made available through the courtesy of Prof. T. D. A. Cockerell, to whom I am indebted not only for this kindness but for many other acts of good will and cooperation throughout the years, including the donation of many specimens that have been helpful in this study. The meliponid fauna of British Guiana has been supplemented still further by material acquired from A. S. Pinkus, and especially by the specimens col-

lected by W. G. Hassler on the upper Essequibo, Kuyuwini, and Shudihar rivers while on the Terry-Holden Expedition in 1937. To Dr. William Holden I am grateful for making this collection accessible.

Additional stingless bees from British Guiana were collected by Mr. Herbert Lang and were kindly lent to me by Dr. George Salt along with specimens of his own collecting in Colombia, specimens that were not only interesting in themselves but that had special significance because they were associated with the informing paper on the biology of stingless bees that Dr. Salt published in 1929.

From Venezuela Dr. J. Anduze has kindly donated specimens, and Dr. G. H. H. Tate has supplied others collected in the course of his expedition to Mt. Roraima in 1927-1928. Mr. H. S. Fleming, a member of Dr. William Beebe's expedition, also generously supplied stingless bees from Venezuela. Particularly am I indebted to Mr. R. G. Donald, who not only has supplied me with stingless bees from Trinidad Island but has accompanied them with valued field notes and observations. As this paper goes to press I am in receipt of five species of Venezuelan Meliponidae, with accompanying data, from Mr. Vincent A. Baker.

One of the most valued collections contributed to the preparation of this monograph is that kindly donated by Dr. W. Weyrauch, mostly from Valle de Chanchamayo in Peru. The worth of this collection for the purposes in hand is greatly enhanced by the wealth of field notes and photographs with which it is accompanied and which will be found scattered here and there through the pages that follow. My thanks are due also to Dr. H. Bassler for specimens this indefatigable collector took in Peru and elsewhere.

To Dr. T. H. Frison I am under obligations for submitting for study his private collection of mostly Brazilian specimens, gathered largely by H. Parish in the course of his travels. Other Brazilian specimens collected in the State of Matto Grosso by Mark Taylor were kindly made available by Prof. T. B. Mitchell, as well as specimens from Panama. To Padre J. Moure and Dr. H. Sick I am indebted for sending some specimens from the southern part of Brazil. The studies of Padre Moure on the stingless bees have also been a

stimulating influence. It is a matter of regret that his recently published papers (1946a, 1946b), as well as a paper by Warwick E. Kerr (1946), have reached me too late to be discussed in the present monograph.

Dr. J. Bequaert has always courteously borne in mind my interests, and his field trips to South and Central America have yielded many interesting forms that I have been happy to study.

Mr. Phil Rau was kind enough to send me specimens collected by him on Barro Colorado Island, Canal Zone (these figure in his book of 1933), and subsequently from Mexico. From the latter country I have also had successive sendings of valued material from Dr. A. Dampf, and recently Prof. T. C. Schneirla has earned my gratitude by contributing specimens obtained in the Mexican State of Oaxaca. Also, I am indebted to Mr. Frank M. Johnson, who with unfailing kindness and forethought directed the Mexican collector, Señor M. Guerra, to be on the watch for stingless bees in the course of a collecting trip supported by Mr. Johnson for the obtaining primarily of Lepidoptera in some of the more southern states of Mexico. Dr. H. O. Wagner has also sent specimens from Mexico.

Specimens have been donated, too, by G. K. Christian from Colombia and by M. Bates from Honduras. Also, I have been the recipient of some specimens collected along the coast of Central America by the Temple Crocker Expedition of 1932 and the "Zaca" Expedition of 1938. Dr. F. X. Williams is yet another to whom special thanks are due, for making available specimens not only from Central America, but also from Ecuador.

In wishing to give credit to the many—institutions as well as individual contributors—that have aided this study through the donations and loans of material, I have left unmentioned too long the available material within the American Museum of Natural History itself. The collection, built up during the years, represents the results of successive trips to the New World tropics by different members of the Museum's Department of Insects and Spiders, supplemented by gifts and purchases of specimens. Of those who have participated in these field trips special mention should be made of Dr. F. E. Lutz, for

more than 20 years head of the department, who with Prof. H. E. Crampton made a journey to Kaieteur Falls, British Guiana, about 30 years ago, and who subsequently spent several seasons on Barro Colorado Island, as well as in the El Volcan region of Panama, being accompanied by Dr. W. J. Gertsch on the last-mentioned trip. Dr. C. H. Curran, Dr. W. J. Gertsch, Mr. E. I. Huntington, and the writer all have collected on Barro Colorado Island during more or less extensive sojourns, so that the apifauna from that limited area and the nearby mainland is abundant. Recently, the collections from the Canal Zone and contiguous parts of Panama have been still further extended through the activities of Dr. C. D. Michener; but especially am I under obligations to Dr. Michener, as is the reader, for the valuable observations he made and which I have drawn upon again and again in the course of the following pages.

Mr. E. I. Huntington and the writer spent one vividly remembered and delightful spring in the Cauca Valley of Colombia, collecting specimens there.

By purchase, the American Museum has acquired extensive named material from Prof. H. Friese. Specimens have also been bought from field collectors in Central and South America—R. Lichy, K. Schmith, P. Willim, W. Weyrauch—and a great many specimens have been acquired as a reward for making identifications.

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The literature of the stingless bees is a large one. Undoubtedly further combing of publications would greatly increase the listed titles of the Bibliography, but incomplete as the Bibliography undoubtedly is, no one who may have the patience to peruse the Introduction or indeed any section of this manuscript will fail to note how largely I have drawn on the observations and records of those who have preceded me. The Bibliography itself has been enriched through titles brought to my attention by Dr. Gordon Ekholm, Mr. Herbert Evans, Dr. E. Oertel, Dr. Herbert J. Spinden, and others, but particularly am I indebted to Miss Annette Bacon for her tireless persistence in ferreting out obscure and rather inaccessible publications and in checking the whole literature with consummate accuracy. So fruitful has been her search of the literature that many of the titles that I am able to offer in the Bibliography owe their presence there solely to her enthusiastic search for everything that had bearing on stingless bees, and I cannot

adequately express my appreciation for the devoted way in which she dedicated herself to the task of locating these works that had escaped my search and in checking the record for all pertinent bibliographical data.

For the sake of fluidity in the presentation, citations from reports in foreign languages have been offered in translation. In interpreting passages that originally appeared in Russian, I have had the valued aid of my daughter, Marjorie D. Schwarz. With these exceptions the translations and summaries from foreign works are my own.

The artists who have prepared the drawings for this study deserve special commendation. Their keen perception of form and their technical skill have made real what mere description has often failed to do. I am indebted in no small degree to the following for their faithful renderings: Mrs. E. L. Beutenmüller, Miss Elena Feld, Mrs. Alma Fröderstrom, Miss Alice Gray, Mr. V. Pierre-Noël, Mrs. Shirley H. Risser. Photographs, too, have contributed not a little to the clarification of the text. Several of the pictures were obtained from H. von Ihering's interesting account of the biology of the stingless honeybees of Brazil (1903), as well as from publications by Silvestri, Huber, Marianno, and others. Photographs furnishing the basis of other pictures in this study were kindly lent me by A. E. Emerson, V. W. von Hagen, F. E. Lutz, O. E. Shattuck, W. Weyrauch, and by my daughter, Dorothy M. Schwarz.

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To Miss Ruth Tyler, Editor of the Scientific Publications of the American Museum, I am deeply indebted for aid and counsel in the physical preparation of the monograph, for giving it final authoritative supervision, and for directing its passage through the various stages from manuscript to printed work. To her has fallen the task of preparing the Index, and the reader, as well as the writer, is under obligations to her for the painstaking thoroughness with which this task has been done.

Finally, having begun this section with an expression of my gratitude to Dr. F. E. Lutz for first making me aware of the riches of interest offered by the stingless bees and so prompting me to undertake this work, I desire in closing to extend my warm appreciation to his successor as Chairman of the Department of Insects and Spiders in the American Museum of Natural History, namely, Dr. Mont Cazier, who has been no less helpful in facilitating my studies of this group and in so arranging the work of the department as to make possible the maximum of clerical assistance in completing the final phases of the task.

HERBERT F. SCHWARZ

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INTRODUCTION: STINGLESS BEES AND THEIR WAYS

THE MELIPONIDAE OR STINGLESS BEES present many points of interest. It has been estimated that only about 5 per cent of all of the thousands of species of bees that occur on this globe are definitely colonial or social. The stingless bees belong to this distinguished minority, which will always prove intriguing to man because he feels prompted to draw comparisons, however unwarranted, between these insect states and his own structure of society. Yet in spite of the elaborations of social life and the changes necessitated by these complexities, the stingless bees have in the main retained the primitive method of feeding their offspring that characterizes the so-called solitary bees, and thus they evidence a behavior link with this extensive and diversified group. In contrast to the honeybee, *Apis mellifera* Lin-

naeus, which thrives nearly everywhere, and the bumblebees, which are so well represented in the temperate regions and survive even at relatively high altitudes and latitudes, the stingless bees seem to be capable of continued existence only in the tropics or at most the subtropics, succumbing to our northern winters when transplanted. The very fact that they are stingless raises a host of questions both practical and disinterestedly scientific. Their nests have enough points of resemblance and also of difference when compared with the nests of the other social bees to invite speculation. Finally the anatomy of these bees and the ways in which they depart structurally from the other social forms and specifically from one another offer fruitful fields for investigation and study.

STRUCTURAL CHARACTERS

The Meliponidae are frequently differentiated from other bees on the ground that the transverse cubital veins of their wings are either obsolete or obsolescent, and in many respects this is a convenient and, on the whole, practicable way of readily recognizing members of this family. But certain of the Halictidae, in other characters very different from the Meliponidae, also show a degeneration of the transverse cubital veins, although not nearly to so marked an extent as in most Meliponidae. On the other hand, in a very few meliponids (more particularly some of the forms grouped in *Trigona* subgenus *Paratrigona*) these veins are rather clearly delineated.

Some species (especially certain members of *Trigona* subgenus *Hypotrigona*) have the marginal cell rather widely open, but even in stingless bees other than *Hypotrigona* the marginal cell tends to be briefly open or there is usually traceable at least a slight enfeeblement of the marginal vein towards the apex.

Like the Apidae, Bombidae, and Euglosidae, meliponid workers have fringing hairs along the anterior and posterior borders of the hind tibiae, and usually a depression or

flattening in the outer face of these tibiae for the pocketing of pollen. But neither the degree of depression nor the equipment of fringing hairs, an aid in the retention of the pollen load, shows constancy throughout the family. In some subgenera of *Trigona*, for instance, *Scaura* and certain *Paratrigona*, the bordering hairs are so short or few as to raise doubt regarding their adequacy for the task for which they were intended. At the other extreme are *Trigona* subgenus *Trigona* and subgenus *Tetragona*, especially the former, which in addition to simple hairs have feathered hairs along the posterior border of their hind tibiae.

The most ineffectual hind tibia structurally is that of *Lestrimelitta*, which lacks a depressed area entirely and would seem, therefore, without capacity for pollen gathering. However, at least one observer (Fiebrig, 1908, pp. 375, 378) claimed to have seen workers of *Lestrimelitta limão* (F. Smith) returning to the nest pollen-laden. Equally remarkable are the absence also in this genus of a comb anteriorly at the apex of the hind tibia and the absence of a row of spines or spine-like hairs along the apical margin within of this joint. Such a comb and row of

spines are found in all other meliponid workers, although very inconspicuous in some of the species of distinctly small stature.

A pulvillus is present in all stingless bees.

Michener listed (1944, p. 290) among the characters common to the stingless bees:

"Posterior tibial spurs absent; jugal lobe of posterior wing present; labrum three to four times as broad as long; . . . marginal cell

open (or its veins weak) distally, tapering from broad base; pterostigma of moderate to large size, extending well beyond base of vein r; claws of female simple; eyes bare, sparsely hairy in some queens; sting reduced."

It is the absence of a functioning sting in the worker and queen that gives the Meliponidae a unique position among the bees.

PHYLOGENY

FAMILY, SUBFAMILY, AND TRIBES

Even to those interested in family trees, this section is likely to prove dull, for while it is a zestful task to trace structural resemblances between one organism and another under the microscope, and from such studies form theories of relationship, the technical record of such a quest in print is far from stimulating. Hence this section will have appeal for relatively few, especially as the conclusions reached are fragmentary and far from final. Most readers will prefer to skim or skip this section and the one preceding and proceed to those sections of the Introduction which deal not with structure but with habit.

At the beginning of the nineteenth century Latreille (1802a, p. 386) included in the same genus *Apis* both the Old World honeybees and the stingless bees, thus following the lead of Olivier, who had described the New World stingless bee *amalihea* as an *Apis*. Latreille took the position that the stingless bees were more closely related to the honeybee than are either of these groups to the bumblebees and the euglossids, which in the sequence of Latreille immediately preceded *Apis*. With the genus *Apis* he continued to associate the stingless bees in several of the publications immediately following (1803, pp. 48-49; 1804a, pp. 393-394; 1805, pp. 67-68). A few years later, however, we find him employing the names *Melipona* and *Trigona* for the stingless bees (1809, pp. 182-183), although these genera are still retained in juxtaposition with *Apis*, which in turn is preceded by members of the Euglossidae and Bombidae. One infers that Latreille, while continuing to emphasize the near relationship of the Apidae and the Meliponidae, also placed close to

them the other two families of bees that have a distinct corbicula.

Lepelletier (1836, pp. 407-435) classified the stingless bees as a tribe (Meliponites) of what he designates the family Apiarides, mentioning as the other tribe the Apiarites, represented by the genus *Apis*. Thus Lepelletier, as did Latreille, emphasized his belief that honeybee and stingless bee were closely related, certainly more closely than is either to the bumblebees, which he placed in a family by themselves.

The tendency to pair the stingless bees with the honeybee also found favor with Schenck (1874, p. 348), who relegated *Melipona* and *Trigona* to a subfamily of the Apidae, while in yet another family (Bombidae) he placed as one subfamily *Bombus* and as another subfamily the genera *Euglossa* and *Eulema*.

In a "biological family tree" indicating the upward progress to a social life, von Buttel-Reepen (1903a, p. 96; 1915, p. 65) designated the Bombinae, the Meliponinae, and the Apinae as subfamilies at the top of the Apidae. He went on to say (1903a, p. 108) that between the bumblebees and the stingless bees there is no intimate relationship. But although these two groups are in his estimation far apart, he looked upon the colonial structure of the stingless bees as constituting an important step biologically between the Bombinae and the Apinae. Similarly he emphasized (1903b, p. 72; 1915, p. 64) that the three subfamilies, Bombinae, Meliponinae, and Apinae, represent entirely distinct branches of the family tree.

Although Börner (1919, p. 169) placed the honeybees, bumblebees, and stingless bees in three tribes (Apini, Bombini, and Meliponini)

of the subfamily Apinae instead of, as did von Buttel-Reepen, listing each of them as subfamilies of the Apidae, he, too, expressed it as his opinion that they were not immediately related to one another but had branched off on diverging paths from a common hypothetical ancestral stem. Börner's conclusions were based on a study of the mouth parts. Handlirsch (1924, p. 823) adopted these tribes but retained only two of them, the Apini and the Meliponini, in the Apinae, which is the classification adopted also by Weber (1933, p. 662) and is reminiscent of the conclusion arrived at by Lepeletier and presented in a previous paragraph. Berlese (1925, p. 823) also interpreted *Melipona* as a bee standing closest to *Apis* and as constituting along with it the subfamily Apinae. *Trigona* he considered merely a subgenus of *Melipona*.

In the "biological family tree" that Stöckert (1924, p. 226) drew up, the stingless bees are by way of contrast given family rank as Meliponidae, with two subgroups, Meliponae and Trigonae, while the bumblebees, on the one hand, and the members of *Apis*, on the other, are grouped, respectively, as the Bombinae and the Apinae under the Apidae. Yet Stöckert is careful to assert (pp. 239-240) that, in spite of the varying degrees of social instinct that manifest themselves in *Halictus*, *Bombus*, and *Apis*, they nevertheless developed independently of one another, with the result that there is no ground for believing that the *Halictus* species were ancestral to the bumblebees or the bumblebees in their turn were ancestral to the honeybees.

In Wheeler (1928, pp. 16, 96) the stingless bees are given subfamily rank with the Bombinae and Apinae in the Apidae, but in this family Wheeler includes also other bees than these as subfamilies.

In his recent excellent paper on the comparative external morphology, phylogeny, and a classification of the bees (Hymenoptera), Michener (1944, pp. 290, 292) designated the Meliponini a tribe of the subfamily Apinae and assigned to that subfamily also as tribes the Euglossini, Bombini, and Apini. Perhaps in view of his searching study the terminology of the present paper should be revised, but I find it a convenience

to think of a group as large as the stingless bees in terms of a family and have accordingly continued to refer to the subject of the present study as Meliponidae.

It is natural to compare the stingless bees with other social bees like the Bombidae and the Apidae. With the latter family particularly comparison is tempting, for in so many ways the Apidae and the Meliponidae seem to parallel each other. The presence in each of a structurally differentiated queen, the practice common to both families of slaughtering the drones or at least of ejecting them from the hive, the act of swarming engaged in by both, and the building of combs that is characteristic of the Apidae and of most Meliponidae indicate, along with many minor points of resemblance, how similar is the pattern of their lives.

While in these respects the stingless bees seem closer to the Apidae than they do to the bumblebees, they have one habit, however, that sets them apart from both and marks them as being biologically a link between the social bees and the solitary. One of the notable differences of habit between the social Hymenoptera and the solitary is the continuing contact in a social community between adults and larvae. There is progressive feeding, the cells being left open so that the adults can bring the waiting larvae the food on which the latter are dependent. As a rule only when the larvae have attained their full growth are the cells sealed and the larvae permitted to undergo pupation in solitude. This is the procedure in the hive of the honeybee. In the case of the Meliponidae, however, the food for the larvae is packed into the cell in advance after the manner of the solitary bees and, while it has been claimed that the closing of the cells of stingless bees is sometimes deferred (Rayment, 1932a, pp. 9-10; 1935, pp. 539-540), the general procedure is to shut off the larvae from the world and let them feed upon the gathered store of food as inclination prompts them.

GENERA AND SUBGENERA

In spite of common characters among the stingless bees, there are also differences that seem to require their separation into different genera and subgenera. Several years ago (1932a, pp. 231-460, figs. 1, 2, pls. 1-10) I is-

sued a monograph on the genus *Melipona* in the Introduction to which I endeavored to establish (pp. 256-260) a line of cleavage between *Melipona* and the other members of the Meliponidae. The genus *Melipona* is confined to the New World, and the present study is a continuation of the investigation of the stingless bees of the Western Hemisphere other than *Melipona*.

The emphasis in a preceding paragraph on the peculiarities in the structure of the hind leg of *Lestrimelitta* will have prepared the reader for the decision to recognize *Lestrimelitta* as a genus. In addition to the hind tibiae there are other characters (listed in the keys on pp. 168, 171, 172) that seem definitely to substantiate the generic independence of *Lestrimelitta*.

After *Melipona* and *Lestrimelitta* have been separated from the other stingless bees of the Western Hemisphere, there still remains a large number of forms belonging to the genus *Trigona*. These forms tend to group themselves into various subgeneric aggregates. Structural characters separating the different subgenera of *Trigona* are given in the keys (pp. 168-173), which also list those characters adopted in separating *Melipona* and *Trigona*.

In addition to the structural characters, *Melipona* and *Trigona* are separated also through certain divergences in their life history. In *Melipona* the cell that contains a queen cannot be differentiated from one containing a worker or a male. In *Trigona* there is (at least in the vast majority of cases) a specially constructed royal cell that houses the royal caste.

The claim has been made, it is true, that in some species of *Trigona* the brood cells are without differentiation. Ducke (1925, p. 341) repeated the conclusion of H. von Ihering (1912, pp. 1, 4-5, 45) that there are no royal cells in the nests of *Trigona* (*Tetragona*) *silvestrii* Friese and *Trigona* (*Cephalotrigona*) *capitata* F. Smith. H. von Ihering was particularly emphatic in the case of the latter species, but Salt (1929, p. 442) found in a nest of *capitata* variety *zeaxmeniae* Cockerell two queen cells, which "were situated with the male and worker cells in the tiers but were readily distinguishable by their larger size and rounded instead of flat ends."

Ducke (1925, p. 341) was inclined to be-

lieve that royal cells were also absent in his Group I (*Hypotrigona*), but as the queens of only two species (*duckei* Friese and *muelleri* Friese) of *Hypotrigona* were known at the time he wrote, his impression lacks completeness. Moreover, even in *duckei* and *muelleri* the thoracic width of the queen is greater than that of the worker, and it would seem likely, therefore, that her cell has some differentiation of size, even if slight. Both *duckei* and *muelleri* as well as *silvestrii* build brood cells of the cluster type, and the failure to detect royal cells applied particularly to nests of that type, for a description of the character of which the reader is referred to pages 22-24.

However, in the nest of another species that builds in this manner, the Indo-Malayan *Trigona* (*Tetragona*) *iridipennis* F. Smith, there were observed a few cells larger than the ordinary ones and one of them, interpreted as a royal cell, was particularly large (George, 1934, p. 2). Castets (1893, p. 485) gave the dimension of the queen cell of *iridipennis* as 5 mm. as against 3 mm. for that of workers. Yet another Old World species that arranges its cells in clusters, namely, *Trigona cassiae* Cockerell, known also as "kootchar," has a queen cell that is described as "much larger than the worker cells" (Hockings, 1884, p. 153). In the case, too, of the New World *Trigona schrottkyi* Friese, which Ducke included among the builders of brood cells of the cluster type, royal cells have been noted (H. von Ihering, 1903, p. 232). In view of this evidence it seems to me more likely that the failure to detect royal cells in the case of certain species that build in this primitive manner is owing to the fact that these builders belong to species of diminutive stature, in which the differences of size between worker cell and royal cell perhaps are considerably reduced rather than completely obliterated.

It may be noted, too, that in nests of *Trigona* the royal cells are usually located near the periphery of the combs or sometimes even attached to the involucre or its supports, while in nests of *Melipona* the undifferentiated queen cells are seemingly intermingled with the cells of the workers and males. On the other hand, the distinction

is not absolute. The case already cited of *Trigona* (*Cephalotrigona*) *capitata* variety *zexmeniae* may illustrate how difficult it is to generalize.

Another curious distinction is claimed between queens of *Melipona* and queens of *Trigona* (H. von Ihering, 1903, pp. 254-255, 258). Anatomical studies made by H. von Ihering on newly emerged virgin queens of *Melipona quadrifasciata* variety *anthidioides* Lepeletier revealed the fact that the genital organs of these young queens were completely undeveloped and that these individuals could accordingly enter upon their functions only after sufficient time had been allowed for the complete development of the genital organs. Different is the condition in *Trigona*, the queens of which issue from their cells in full maturity. Qualifying this generality is, however, the observation of Salt (1929, p. 435), who found that the ovaries of young females of *Melipona interrupta* variety *salti* Schwarz "were developed though not yet producing eggs."

Contrasts of size are often very striking when comparison is made between the species of small stature that belong to *Trigona* and those of large stature that are assignable to *Melipona*. In plate 6, figure 2, the large *Melipona flavipennis* F. Smith, one of the more robust of stingless bees, is reproduced with *Trigona* (*Hypotrigona*) *duckei* Friese, often referred to as the smallest of all known bees.

One encounters grave difficulties when the attempt is made to construct a family tree of stingless bees. Lutz (1924a, pp. 229-232, fig. 23) offered what he designated as "A diagrammatic conspectus of the principal combinations of characters considered¹ and a provisional outline of their phylogeny." This diagram is here reproduced as figure 1, altered only to the extent that subgeneric names have been inserted at various places in the diagram. Lutz stated frankly (p. 232):

¹ The characters Lutz considered embraced the following alternatives: entire or emarginate scutellum, hairy or naked scutellum, smooth or sculptured mesonotum, partly even or fully toothed mandibles, long or short mouth parts, plain or branched tibial hairs, shape of hind tibiae (whether triangular, oval, bowl shaped, or club shaped), and shape of the apex of the hind tibiae (whether rounded or angular and the degree to which they are angular).

"I do not know whether the diagram is a true picture of the phylogeny of these particular combinations or not. There are facts in the biology, wing-venation, etc., of these bees that indicate *Melipona* as the starting-point of the family, but it may be that *Lestrimellita* [sic] with its nearly cylindrical tibiae and relatively short mouth-parts is closer to the primitive stock. In the latter case the phylogenetic history may be traced from there without changing the diagram. Also, although *Melipona* is so like *Trigona* in most characters that good authorities have united the two genera, even an amateur can distinguish them by differences in their general appearance. It is conceivable, but not probable, that we have here an extreme case of biphyletic origin of an apparently homogeneous group."

Melipona in having undifferentiated cells for its queens as well as its workers resembles *Apis dorsata* while *Trigona*, with its royal cells, tends to resemble such species of *Apis* as *mellifera* and *floreana* and their varieties. This indication of a more primitive stage of development in *Melipona* than in *Trigona* prompts one to place *Melipona*, as Lutz did, at the bottom of the diagram. Yet while this fact, drawn from the biology, supports the interpretation of primitiveness in the case of *Melipona*, another fact, likewise drawn from biology, tends to challenge this interpretation. All known *Melipona* build their brood cells in combs, which is an advanced stage of nest architecture. In contrast, occasional species within the several subgenera of *Trigona*, and possibly a whole subgenus like *Hypotrigona*, arrange their brood cells primitively in clusters. It is especially disconcerting to one endeavoring to construct a family tree to find that among the species of *Tetragona*, a subgenus that on the basis of its plastic characters one would be inclined to place towards the top of a phylogenetic classification of the Meliponidae, there are several species that actually still retain this archaic method of building their brood cells in clusters.

It is possible, of course, as Lutz diffidently intimates, that *Lestrimellita* is the most primitive of the existing stingless bees. The very imperfect equipment of this genus and the fact that in lacking a tibial comb it would

seem to perpetuate a structural deficiency existent in the fossil genus *Meliponorytes* (pp. 8-9) point to such a possibility. On the other hand, there is also the possibility, one might even say the likelihood, that *Lestrimelitta* is, instead, a retrogressive genus that is in process of losing its self-reliant status and heading towards a condition of dependence on its neighbors. It has been so interpreted by some (p. 176). Under such process of degeneration one might expect the loss of characters to parallel that which occurs in the sluggish queen of meliponid species, and meliponid queens throughout the family lack, as in the several castes of *Lestrimelitta*, the tibial comb that in all Meliponidae other than *Lestrimelitta* earmarks (or shall we say legmarks?) the worker.

In view of the uncertainties and contradictions we shall probably do well not to attempt to erect too rigid a family tree of the Meliponidae but, adopting the methods in solving a jigsaw puzzle, to fit together odd bits of the pattern that seem to interdigitate, and to unite these with other contiguous parts, where possible. At the same time it seems necessary to admit that, owing to missing links and gaps, the complete picture in all likelihood cannot be restored.

Standing close to each other are the subgenera *Trigona* and *Tetragona* (in the upper left of fig. 1) which have compound hairs fringing their hind legs posteriorly and show their affinity also through the presence in all of the *Trigona* and in some *Tetragona* of a small, differentiated area of appressed hairs at the base of the inner face of the hind metatarsi. No other subgenera are thus equipped. The subgenus *Trigona* is, furthermore, well armed with teeth along the apex of the mandible, and one is accordingly inclined to give it top place in the family tree of the stingless bees. Because of the significant characters *Trigona* and the subgenus *Tetragona* have in common, one is inclined to place close to *Trigona* the subgenus *Tetragona*, notwithstanding the primitive building methods of certain *Tetragona* (already mentioned) that seem to point to a lower status for this subgenus.

Similarly there can be little doubt, I think that the subgenera *Scaptotrigona* and *Nannotrigona* belong close together (as Lutz has

them). The V-shaped incision at the base of the scutellum is as intimate and as characteristic a link between these two subgenera as the unusual characters that unite *Trigona* and *Tetragona*. I doubt whether *Cephalotrigona* or *Paratrigona* are nearly so closely related to *Scaptotrigona* as is *Nannotrigona*.

In its sculpturing, at least, *Paratrigona* is comparable to many *Hypotrigona* (a subgenus not figured in the diagram), but in other ways it is very different. The few species of *Hypotrigona* regarding which the nests are known build brood cells of the cluster type. In other words, they seem to be primitive at least in this respect. But in another respect, the eccentricity of their wing structure, they represent a degree of specialization that suggests a culmination rather than a starting point in development. The fully toothed mandible of *Paratrigona* seems also in the nature of a culminating development, entitling *Paratrigona* to a high place in the scale, such as Lutz has assigned it.

In the genus *Trigona* it is probably the subgenus *Mourella* that comes closest to *Melipona*. Not only does the structure of the hind leg suggest *Melipona* but, of possibly greater significance, *Mourella* has the hairy propodeum that is found in *Melipona* but is shared by very few subgenera of *Trigona*. *Plebeia* in its general structure stands not far removed from *Mourella*, and close in its turn to *Plebeia* is probably the subgenus *Scaura*, which differs, however, in having a mandible that is edentate and a hind metatarsus that is conspicuously swollen. If, as Lutz's diagram implies, the *Trigona* branched upward from an ancestor in *Melipona* that, like some of the existing members of that genus, had a partly toothed mandible, then it seems more likely that *Scaura* with its greater specialization and therefore greater departure from the pre-supposed ancestral plan should find place above rather than below *Plebeia*. However, it would seem equally logical to speculate that *Scaura* might trace back to an ancestor in *Melipona* or to some *Melipona*-like extinct genus in which the mandible was edentate as in most existing *Melipona*.

I am disinclined to believe that *Partamona* is as closely associated with *Plebeia* as the diagram seems to indicate. More likely does it seem to me that *Partamona* belongs to a

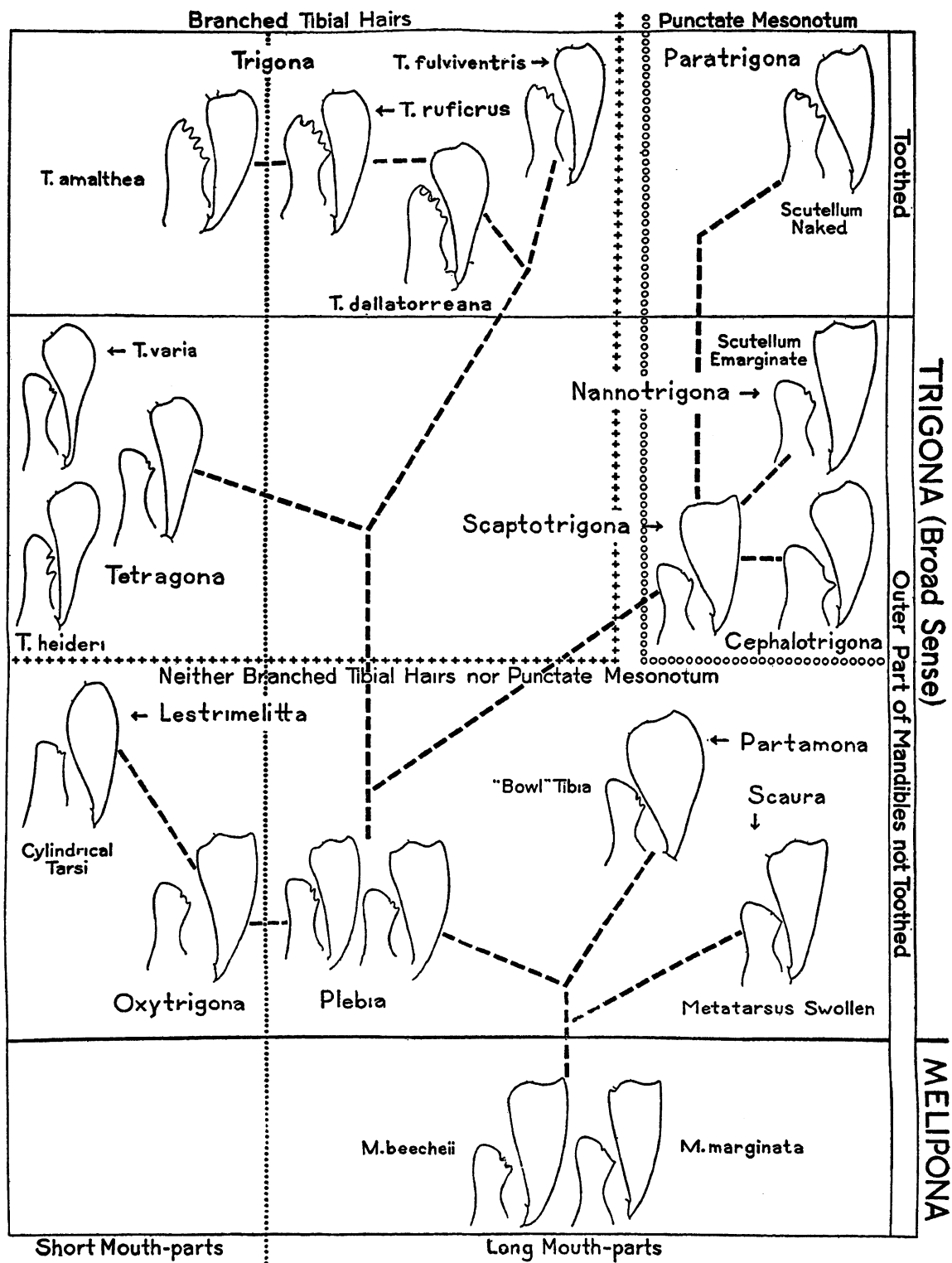


FIG. 1. A provisional outline of the phylogeny of the stingless bees as prepared by F. E. Lutz, with subgeneric names added subsequently.

branch of the family that includes such subgenera as *Schwarziana* and *Parapartamona*. *Schwarziana* in certain respects seems to point back to *Melipona* or a *Melipona*-like ancestor. The character of its sculpturing, the relatively large number of hamuli in its lower wing, the presence of hairs in the middle region of its propodeum as well as on the sides give support to this interpretation. But its hind tibiae, flattened to slightly depressed as they are in the worker from the apex almost to the base, seem to me to point the way to the type of spacious and deeply excavated tibiae that, more fully developed in the subgenus *Parapartamona*, reaches its culmination in the subgenus *Partamona*. It is in order to indicate that *Partamona* is the only subgenus of smooth chitin that has the middle region

of the propodeum hairy. Of the subgenera of sculptured chitin that share with *Melipona* and *Partamona* this hirsute condition, only *Mourella* has characters that seem to ally it with *Plebeia* rather than, as in the case of the other two, *Schwarziana* and *Parapartamona*, remotely with *Partamona*.

The diagram places the subgenus *Oxytrigona* close to *Lestrimelitta*, but I question whether these two rather eccentric members of the Meliponidae have any close relationship to each other. *Lestrimelitta* is so sundered in many ways from the other members of the family that its affiliations are almost impossible to establish. And *Oxytrigona*, too, with its unusual methods of defense and its odd structure, is hard to place with confidence at any given place on the family tree.

DISTRIBUTION

FOSSIL RECORDS

There have been various attempts to interpret as relatives of the Meliponidae certain bees found in amber. Burmeister (1832, p. 636) referred to a small form from Baltic amber of the Lower Oligocene (Handlirsch, 1907, p. 892) which seemed "to have affiliation with the native South American genus *Trigona*." Brischke (1886, p. 278) commented on "two bees which in their venation remind of the South American genus *Melipona* but differ in the structure of their legs." These likewise were from Baltic amber of the Lower Oligocene (Handlirsch, 1907, p. 892).

Yet these early interpretations have been challenged. Cockerell (1910a, p. 6) was inclined to reject the generic references as "quite worthless." On the other hand, he did single out for praise, as the only amber bee up to then properly described, *Meliponorytes succini* Tosi. This bee, as well as another species (*sicula* Tosi) referred likewise to *Meliponorytes*, was found in Sicilian amber, which dates from the Middle Miocene and is accordingly of later age than the Baltic amber. Cockerell believed that *Meliponorytes* was very close to the modern *Trigona*. Tosi (1896, pp. 352-356), on the other hand, thought its affiliations were in some respects with *Trigona* and *Tetragona*, in others with *Melipona* in the limited sense. Its habitus is per-

haps a little closer to that of *Trigona* than to that of *Melipona*.

Considering first *Meliponorytes succini*, which is more fully described and figured by Tosi (1896, pp. 352-356) than *M. sicula*, it may be emphasized that the description indicates that the wings surpass the abdomen in length, and this description is substantiated by the representation of the insect on plate 6 of Tosi's article. However, it must be admitted that the extension of the tip of the wing beyond the apex of the abdomen is not impressive and that with respect to wing length one might have some hesitancy in assigning the specimen either to the relatively shorter winged *Melipona* or to the relatively longer winged *Trigona*. Judging from the drawings the stigma is rather *Melipona*-like than *Trigona*-like.

Certain other wing characters are shared by *Meliponorytes succini* with recent stingless bees. Thus its marginal cell just fails of completion, being barely open at the apex, a condition which is fairly general in the Meliponidae although subject to exceptions. Again, the first transverse cubital vein is feebly demarked, the second absent. In recent stingless bees the transverse cubital veins show various degrees of degeneration, and almost always when one of the two transverse cubital veins is a little more clearly delineated

than its fellow, this distinction applies to the first transverse cubital.

The inner surface of the hind tibiae of *M. succini* slants roof-like to each of the sides of the joint, as in *Melipona* and several subgenera of *Trigona*, and there are other characters which substantiate the probable affiliation of this fossil insect to bees of the family Meliponidae. As convincing as anything in this connection are the fringing hairs on the hind tibiae forming a corbicula, the shape of the posterior metatarsi, the relative length of the hind metatarsi compared to the combined small tarsal joints, the longer hairs on the scutellum compared with those of the mesonotum, the general appearance of the abdomen, and the like.

The prominence of the lateral ocelli of *succini*, as indicated in Tosi's figure of the head and in his description, and the suppression of its middle ocellus in a sulcus are in accord with the condition found in many *Trigona*. If, however, I interpret the drawing of the head correctly, the lateral ocelli are not so obliquely placed as in most stingless bees, and their slant in the drawing is, if anything, inward rather than, as in most stingless bees, outward.

While *Meliponorytes succini* has much in common with recent stingless bees, there are also characters that set it apart. A character at variance with what is usual in the Meliponidae is the presence of what in the drawing of the head suggests two denticles (referred to in Tosi's description as two sulci) on the outer half of the apex of the mandible instead of the inner half. In recent stingless bees when denticles occur on an incompletely toothed mandible, they are along the inner one-third of the apex.

The second species (*sicula*) that Tosi referred to *Meliponorytes* is not so adequately figured as *succini*. Again the mandible is referred to as having two light sulci at the extremity. The marginal cell in *sicula* is stated to be open at the end as in *succini*, but the stigma is lacking and, because of this, Tosi believed *sicula* related to *Melipona* in the limited sense.

So far as the description and the figures indicate, neither *succini* nor *sicula* has a comb anteriorly at the apex of the hind tibiae which characterizes all recent stingless bee

workers except those assignable to *Lestrimelitta*.

H. B. von Buttel-Reepen (1915, pp. 10-11) found in amber two specimens of bees that seemed to him to represent an intermediate stage between the stingless bees and the honeybees. This transition form he named *Apis meliponoides*.

GEOGRAPHICAL RANGE

The Meliponidae are essentially a group of tropical distribution, with extensions here and there into the subtropical regions. In Africa stingless bees have been reported from the Sudan (Theobald, 1906, pp. 87-88) and from Abyssinia to the east of the Sudan (Gribodo, 1879, p. 340; Alfken, 1932a, p. 54). Westward from these regions they doubtless occur in French Equatorial Africa and have been found in the Cameroons, Nigeria, Liberia, and Sierra Leone, and southward in the Belgian Congo, Kenya, Tanganyika Territory, Angola, Northern and Southern Rhodesia, Southwest Africa, the Transvaal, Mozambique (Cockerell, 1934b, pp. 46-62). Thence, crossing the wide Mozambique Channel, they reappear in the Island of Madagascar (De Saussure, 1890, pp. 4-5). They have representation in India and Ceylon and occur with increasing density in the Netherlands East Indies, northward through the Federated Malay States and Indo-China, with species in the Philippines and Formosa (Schwarz, 1939c, pp. 83-141). I have even seen a specimen allegedly from Japan. Still moving eastward, one encounters their colonies in New Guinea (Friese, 1908a, pp. 357, 358; 1909b, pp. 271-278) and Australia. They have been reported from Northern Territory and are well represented in Queensland from the Cape York Peninsula southward; New South Wales as well as South Australia harbor species (Cockerell, 1930b, p. 150). Rare are the records from Western Australia, possibly owing to inadequate collecting (Rayment, 1935, p. 740). Rayment commented (1932a, p. 183; 1935, p. 510) that in Australia *Trigona* extend at least as far south as Sydney. According to Girard (1879, p. 726) a *Trigona* was represented among the material sent by Tasmania to the World's Fair held at Paris in 1855, but it is doubtful whether this record is accurate.

Far to the north of the Australian region in the Palau Islands, lying about 10° east of the Philippine Island of Mindanao, there is also representation of *Trigona* (Yasumatsu, 1935, p. 94; Schwarz, 1939b, pp. 151–152; Cockerell, 1939a, pp. 61, 62). In the Caroline Islands these bees are known to occur as far eastward as Truk Island, which is roughly in the same longitude as the Bismarck Archipelago, and finally outposts of the Meliponidae have been reported from New Georgia, Guadalcanal, and Binskin Island, of the Solomon group (Cockerell, 1911b, p. 176; 1936d, p. 225). But from about longitude 160° E., which roughly bisects Guadalcanal, one may travel eastward through the great stretches of the Pacific without coming upon further insular representatives of the stingless bees. At any rate, if members of the family Meliponidae exist on any of the specks of land dotting this vast expanse of ocean, they have as yet escaped the net of the collector or the notice of the trained observer.

Not until one reaches the west coast of South America do these bees again reappear, to attain their greatest abundance and variety in the New World. With the exception of Chile they are known with certainty from all the countries of South America, although in Argentina they would seem to be confined to the more northern half of that state. One is considerably puzzled regarding their alleged presence in Chile. Herbst (1921, p. 102) stated emphatically that they do not occur there, rejecting the claim of their presence made by Gribodo (1895, p. 201) as fallacious. My own inclination has been to accept the interpretation of Herbst, for I have never come upon stingless bees among Hymenoptera forwarded from Chile. However, it is a little bewildering to encounter the following statement in the narrative of the seventeenth century missionary Vázquez de Espinosa (1942, p. 737). In speaking of the city of Castro, "the last in the kingdom of Chile before the Straits" and "built on the largest island in the Chiloe Archipelago, at 43° S.", the observant friar noted: "All through the woods and forests there are in the trees great numbers of hives of excellent honey, made by the many varieties of bees to be found on those islands." If his observation was authentic, one is almost forced to the conclusion that stingless bees

were numbered among the honey producers of the region. "Many varieties" suggests native bees, not the introduced honeybee of the Old World, and the reference to the nests as arboreal strengthens the impression that the bees belonged to the stingless group. However, there are also wasps that produce honey and, because of this continuity of habit in two different suborders of the Hymenoptera, it is possible that Vázquez de Espinosa interpreted as bees what were, in fact, social wasps.

From South America the meliponid fauna extends northward throughout Central America into Mexico, and a few forms have established themselves in certain of the West Indian islands, especially those not too remote from the continental land masses like Trinidad and Tobago, while in such islands of the Leeward group as Dominica, Guadeloupe, and Montserrat, there is still a thinning representation. Cuba and Jamaica have a single species of the family.

It is possible that more intensive entomological exploration of Haiti may reveal the presence of stingless bees there, for, as noted elsewhere in this Introduction, Columbus obtained wax, possibly that of stingless bees, during his sojourn on this picturesque island (Belknap, 1792, p. 118), but no trace of the actual bees has as yet been found. From Puerto Rico, the Virgin Islands, the northern representatives of the Leeward Islands, not to mention the Bahamas, stingless bees are unknown.

The fact that stingless bees are so poorly represented in the insular apifauna of the West Indies may perhaps be explained by their habits, especially if it be assumed that many insects owe their insular dispersal to the agency of hurricanes. Solitary bees thus whirled to another homeland would more readily establish themselves, aided by the fact that all the females are potential layers of eggs, thus assuring a new generation. But in the case of the stingless bees the queen, on whom the colony is dependent for its egg supply, is a homebody, confined, except for one or possibly two occasions in her lifetime, to the interior of the nest.

If a colony were in the act of swarming and were carried as a unit (queen and workers included) to an insular outpost, there would be

some assurance of a successful establishment of the species there. But the buffeting of the winds would very possibly prevent such cohesion. Of course, as shown elsewhere (p. 160) stingless bees are hardy travelers, and possibly some colonies have reached their destinations afloat in a hollow log, while it may be contended that in other instances former land bridges have facilitated the passage.

In the southern part of their New World range stingless bees reach the subtropical parts of south Brazil, the adjacent Misiones region of Argentina, as well as Paraguay and Uruguay. At the northern extension of their distribution stingless bees are well represented in southern Mexico, but due to inadequate collecting, it is difficult to state their northern limit in that country. More than 100 years ago, Hall (1824, pp. 224-226), in the course of a voyage along the west coast of Mexico, reported seeing a stingless bee nest at Tepic, in the present Mexican State of Nayarit. From Tamazunchale, in the State of San Luis Potosí, which has almost the identical latitude of Tepic but is close to the east coast of Mexico, I have recently received through the kindness of Dr. H. O. Wagner some stingless bees of the subgenus *Scaptotrigona*. If one continues in approximately the same latitude eastward, one reaches the northern fringe of Yucatan, from which stingless bees have been reported several times. Thus, one can say with assurance that Meliponidae occur both in the west and east of Mexico, at least to approximately latitude 22° N., with the likelihood that they are represented well north of this latitude in propitious localities.

Among sites much farther north favorable to the establishment of stingless bees can probably be included some of the barrancas of southern Sonora. These barrancas "have been penetrated by many species and genera (of plants) which are associated with tropical vegetation."¹ Sapper (1935, p. 188) indicated that bee-keeping had extended to this area, citing (p. 189) V. A. Reko to the effect that in a publication designated *Arte*

de la lengua Cahita, first issued in 1620 and reprinted by Eustaquio Buelna in Mexico in 1890, reference is made to the "tame bee of the hive," a phrase probably to be interpreted as a stingless bee. The Cahita are a group of Piman tribes, consisting mainly of the Yaqui and the Mayo. Their homeland is in southwestern Sonora and northwestern Sinaloa, Mexico, especially in the middle and lower portions of the valleys of the Río Yaqui, Río Mayo, and Río Fuerte. Various other bees are also listed according to Sapper (pp. 189-190) in the work just cited. While it is interesting to be told that the "tame bee of the hive" was domesticated in these Cahita areas, it would be even more interesting to receive specimens of wild Meliponidae from these regions as confirmation of their presence. So much for the west coast of Mexico. As for the east coast, the rapidly diminishing rainfall between Tampico and Brownsville does not suggest ideal conditions for stingless bees. Whatever the northern limit for these insects in Mexico may be, one can say with some confidence that they fail at least to attain even the southern fringes of the United States, although some social Hymenoptera, like *Nectarina lecheguana* (Latreille) of wide distribution in the tropics, have representation in the Brownsville area of Texas.

Associated especially with the moist tropics, and particularly partial to the rain forests, stingless bees nevertheless are found every now and then in areas that are semi-arid. Thus at Acapulco, Mexico, I collected several species of stingless bees, notwithstanding the fact that the environment seemed unpropitious, and in semi-dry localities in Panama they also seem here and there to persist. Probably the same penetration of outlying areas, even if seemingly somewhat unfavorable, takes place throughout their range. But, in spite of such exceptions, the humid tropics seem to furnish the best conditions for the wellbeing of these bees, and it is there that they are most abundant.

ABUNDANCE OF SPECIES IN GIVEN AREAS

Intensive collecting in a given region may reveal the presence of a large representation of species of stingless bees. Thus Ducke (1906b, p. 59) recorded 42 species from the neighborhood of Belem do Pará, Brazil, and I

¹ Cited from the foreword by Forrest Shreve from "Rio Mayo plants," by Howard Scott Gentry, 1942, Carnegie Institution of Washington, Publ. 527, pp. 1-328, pl. 2-29.

have myself listed (1934, pp. 1-23) from Barro Colorado Island, Canal Zone, which has an area of only about 3840 acres, no fewer than 26 species and subspecies of Meliponidae. This is a rather impressive concentration of species when consideration is given to the fact that Lutz and Cockerell (1920, pp. 492-502) listed a total of only 66 species and subspecies from all Central America, Mexico, and the West Indies.

Local concentration of species in a small area is well exemplified in a summary by Michener (1946, pp. 180-181) based on observations made among the ruins of Old Panama in Panama, famous as the scene of Morgan's raid but perhaps now destined to

species represented by a total of 36 nests had all of these established within three zones, two of which were the same as those in which the preceding species had its greatest representation.

Michener stated: "Areas A and B are adjacent to a rather large mangrove swamp, a small coconut grove, and a considerable area covered with brush and small trees. Area D contains a considerable number of trees and is adjacent to some partly wooded land. It is suspected that the sources of food thus provided explain the large number of nests in these areas. The other areas are largely surrounded by grasslands with few trees."

He may be right in his conclusions, but I

ZONE	A	B	C	D	E	TOTAL
<i>Melipona favosa</i> var. <i>phenax</i> Cockerell	3	4	0	3	1	11
<i>Melipona interrupta</i> var. <i>triparidis</i> Cockerell	1	1	0	0	0	2
<i>Trigona</i> (<i>Nannotrigona</i>) <i>testaceicornis</i> var. <i>perilampoides</i> Cresson	26	20	1	2	0	49
<i>Trigona</i> (<i>Tetragona</i>) <i>jaty</i> F. Smith	6	3	3	11	6	29
<i>Trigona</i> (<i>Partamona</i>) <i>testacea</i> , undescribed var.	11	6	0	19	0	36
<i>Trigona</i> (<i>Tetragona</i>) <i>nigra</i> var. <i>paupera</i> (Provancher)	0	4	0	3	0	7
<i>Trigona</i> (<i>Scaptotrigona</i>) <i>pachysoma</i> Cockerell	1	0	0	4	0	5
<i>Trigona</i> (<i>Trigona</i>) <i>fulviventris</i> var. <i>fulviventris</i> Guérin	0	0	0	1	0	1
<i>Trigona</i> (<i>Trigona</i>) <i>corvina</i> Cockerell	0	0	0	1	0	1
	48	38	4	44	7	141

become equally famous because of the successful invasion of the bees. The terrain examined was about one-quarter of a square mile in area. Within that relatively restricted space Michener located no fewer than 141 meliponid nests, most of them along two sides of the square. In a letter he commented to the effect that many nests must have been overlooked because they belonged to species with inconspicuous nest entrances or were located high up in walls that were still standing, but even without making allowance for these putative additions to the total, it is evident that in this area the stingless bee population was impressively large. He divided the area into five zones designated by letters, and it is a matter of interest that the species of greatest abundance, accounting for 49 of the total of 141 nests, was preponderantly confined to two of the five zones, while another

prefer to think that proximity of a suitable nest site rather than consciousness of the accessibility of sources of food prompts the selection of a new home by an emerging swarm. My own interpretation inclines to the view that the concentration of populations in certain of the zones points possibly to the founding of daughter colonies from parent colonies already established in those zones or from the wild land immediately contiguous.

A contributor to the American Bee Journal (Anonymous, 1889, p. 387) mentioned a traveler in Mexico who in one day had found upwards of 100 swarms of stingless bees, 25 of which were located in a single wild fig tree. Possibly the record is authentic, but one is a little prejudiced because the author lumps the stingless bees of Central and South America under the amazing designation "*Aphis meliphona*."

In the narrative of Antonio Vázquez de Espinosa, a Carmelite friar who traveled from the northern end of South America southward as far as Paraguay, Argentina, and Chile, there are several exuberant statements regarding the abundance of bees and honey, of which the following (1942, p. 77) may be cited as an example:

"The Río de Maicaguáin,¹ though small, is very attractive; along its banks are handsome shady glades with various kinds of trees, in which, and in those of the whole region,

there are countless hives of excellent honey, which various sorts of bees make from flowers of great medicinal value and there are quantities of wax; in fact, all the hollows, trunks, and branches are loaded with honeycomb, and the Indians collect a great deal, both for their sustenance and for the production of the honey wine they drink, and also for trade with the Spaniards."

Thus in earlier historic times as well as more recently honey was, and still continues to be, locally at least, very abundant.

CONCERNING NESTS

NEST SITES

In the choice of a nest site stingless bees taken as a whole show great adaptability. Even a given species or a variety of a given species may evidence considerable latitude in selecting places deemed suitable for the establishment of a colony. In contrast other species, however, are, locally at least, so constant to a particular kind of shelter that one is inclined to wonder whether such local groups constitute biologic races.

In general the nest site preferred is some hollow, and usually such a hollow is in a tree, often in the trunk, more rarely in the branches, occasionally in the roots. Nests are sometimes located not far above the ground; in other instances they are placed well beyond the reach of those traversing the forest floor. Arboreal nests are usually enclosed and therefore completely concealed except for the portal of admission, but there are instances, too, in which the nests are exposed or at least partly exposed. Such externally placed nests may be supported by a branch, or wedged in between the forking of two limbs, or sheltered by a bromeliad (pl. 1, fig. 1) or other epiphytic plant that has found lodgment upon the tree. In some instances the space accommodating a sheltered nest may be inadequate, with the result that only the brood chamber is in the hollow and the other nest parts bulge out externally like the exposed top of a charlotte russe.

From the use of arboreal hollows it is only a step to the occupation of any convenient

hollow. Spaces within the walls of buildings, whether these buildings be of wood or stone or some other material, are favorite nesting places. Natural excavations in the rocks may also meet with approval.

Instead of erecting arboreal nests or nests in walls, other species build their nests in the earth. Some of these species are only occasionally subterranean, *Trigona* (*Trigona*) *fulviventris* Guérin, for instance; others are predominantly subterranean; while a few *Trigona*, such as *Trigona* (*Schwarziana*) *quadripunctata* (Lepeletier) and *Trigona* (*Trigona*) *mombuca* variety *subterranea*² Friese, may even be exclusively subterranean. We say "may even be" because, while the existing records point to this possibility, they are hardly numerous enough to form the basis of a positive conclusion. According to Guenther (1931, p. 298) bees which nest in the ground are known as "baira," "ira" meaning honey and "ubu" signifying earth. Thus the combination "baira" expresses the idea of earth honey.

Subterranean nests are sometimes located at very great depths in the earth. According to H. von Ihering (1903, p. 232) a nest of *Trigona* (*Tetragona*) *mombuca* variety *subterranea* Friese which he excavated at Ypiranga, State of São Paulo, Brazil, was at a depth of 3.3 meters beneath the surface, "almost perpendicularly below the entrance hole although the tunnel of approach led down in spiral windings of irregular diame-

¹ According to Vázquez de Espinosa this river is one of those "lying between the Orinoco and the Marañón."

² Moure has placed this species and some of its near relatives in a new subgenus, *Geotrigona*, rather than in *Tetragona* (Moure, 1943, p. 146).

ter." The same species may, however, nest much nearer the surface. Thus Bertoni (1911, p. 142) recorded a nest of *subterranea* which was only 80 centimeters down in the earth. Similarly H. von Ihering (1903, pp. 227-228) described a nest of *Trigona* (*Schwarziana*) *quadripunctata* variety *quadripunctata* (Lepeletier) which extended into the depths for 3 meters, while in contrast nests of the same bee examined by Bertoni (1911, p. 142) had a depth generally of no more than 30 to 50 centimeters.

When bumblebees make their nest in the ground, the spot selected is usually the deserted nest of some small mammal—field mouse, mole, or chipmunk. What is the practice of the ground-nesting meliponids? Do they tunnel into the ground and thus create their own environment or do they, too, occupy a shelter that has been fashioned by some other creature? The question requires more field observation before an answer can be given that will have full validity, but it is safe to say that in some cases at least the site chosen by the stingless bee colony has previously served as the nest of some earlier occupant. Only the earlier occupant in the cases recorded is not a rodent, it is an insect. Marianno (1911, p. 81) found several nests, six in all, of *Trigona* (*Schwarziana*) *quadripunctata* variety *bipartita* (Lepeletier) that covered the space formerly occupied by an enormous nest of the fungus-growing ant, *Atta sexdens*. He expressed the belief that the bees had installed themselves in the deserted formicary of the ants. This surmise receives confirmation in the observations of W. Weyrauch, who found several instances of two species, *Trigona* (*Paratrigona*) *lineata* variety *nuda* Schwarz (pl. 7) and a member of *Trigona* subgenus *Partamona*, nesting in the abandoned underground fungus chamber of this very ant. Thus members of at least three different subgenera of *Trigona* seem to share a preference for the nests of *Atta sexdens*. Again and again reminders of this kind, whether it be of bodily structure, of nest architecture, of shared predilections, or common habits, manifest themselves from group to group within the stingless bees to emphasize the fact that, even though there are lines of cleavage, there are also strong resemblances among the different component

genera and subgenera of the family.

Just as ant nests located in the earth seem to have lured some species of *Trigona* into establishing subterranean abodes, so other *Trigona* have been tempted to go below the surface because of the presence in the earth of a termite or "white ant" colony that seemed suitable for the reception of a nest of stingless bees. Yet the interest of *Trigona* bees in colonies of termites is by no means limited to the terrestrial associations of these insects. Arboreal termite structures, those of several species of the genus *Nasutitermes*, for instance, are places of residence favored by some stingless bees, notably *Trigona* (*Scaura*) *latitarsis* Friese. Another termitophilous stingless bee is *Trigona* (*Paratrigona*) *impunctata* (Ducke) (pl. 8), and *Trigona* (*Trigona*) *fulviventris* Guérin and its variety *guianae* Cockerell manifest frequently a partiality for nest sites prepared for them by the cooperative termites. Indeed the termitophile habit of stingless bees is not only pronounced but widespread. In some subgenera of *Trigona* association with termites is the nesting habit that is predominant; in other subgenera it reveals itself only occasionally in this species or that. Sometimes it is locally very characteristic of a given species, *Trigona* (*Trigona*) *amalthaea* (Olivier), for instance, in parts of Costa Rica, but may not be shared, or may not be shared in the same degree, by members of the same species established in other regions.

The partiality for termite nests as places of abode is not confined to certain New World species. In the Old World, too, this association has been reported, notably so in the case of the African *Trigona clypeata* variety *clypeata* Friese and *Trigona clypeata* variety *zebra* Friese (Morstatt, 1921, pp. 287-290), although mentioned also in connection with *Trigona ruficornis* F. Smith (Horne, 1870, p. 185), later renamed *smithii* (C. T. Bingham, 1897, p. 563), and *Trigona* (*Tetragona*) *iridipennis* F. Smith (Castets, 1893, p. 481, and 1908, p. 52). Nor is the association entirely confined to species of *Trigona*. In Old Panama, Panama, C. D. Michener wrote me, one nest of *Melipona favosa* variety *phenax* Cockerell was obviously built, at least in part, in a small termite nest.

While the fidelity of certain species of

Trigona to the colonies of termites tends to bring into prominence the termitophilous inclinations of stingless bees, other Apoidea, too, are not disinclined to avail themselves of the hospitality offered by termitaria. Thus Horne (1870, p. 181) records the following of *Apis florea* Fabricius, which he refers to incorrectly as *Apis floralis* Fabricius: "I have occasionally found nests of this species built in the interior of mud walls, in the cavities between bricks or in the hollows excavated by *Termites*."

Another and even more interesting reference occurs in Hughes (1933, p. 184). Speaking of the birds known as the honey guides (see p. 97), Hughes stated: "They will also guide to honey in hollow deserted 'Mafwesa' antheps on the flats, where trees are scarce or none at all. These can sometimes simply be kicked over, exposing the combs." The combs in the picture that Hughes supplied (1933, fig. opposite p. 184) of an overturned termite nest harboring a colony of bees I interpret as those of a species of *Apis*. By "antheps," it would seem, Hughes means termite structures.

Strange as is this association of two colonial insects, bee and termite, it seems to be on the part of the termite an involuntary acceptance of a tenant and on the part of the bee a case of squatter's sovereignty. There is in the association no sinister implication such as obtains, for instance, in the case of the ant genus *Carebara* and the termite neighbors on which it preys.

Termite nests from 4 to 6 or 7 feet high were encountered by James W. Wells (1886, pp. 127-128), in great numbers on a journey up the valley of the Rio Sapão in the State of Bahia, Brazil, and, according to that traveler, "certainly one out of every three" such nests was occupied by the "abelha de cupim" (bee of the white ants). Wells was under the impression that in the majority of cases the bees had driven out the termites. Although several dozens of the termite mounds were examined, in only two or three instances was it found that a mound that had been taken over by the bees was still tenanted also by the termites. On the other hand, Drory (1874, p. 282) recorded the receipt of a colony of *Trigona* (*Scaura*) *crassipes* (= *longula*); but in this case the bees died out,

and the termites with which they were associated continued to survive.

The partiality of some stingless bees for termite nests as a place of abode has given origin to the native name, "cupira," which was adopted by F. Smith as the scientific name of one of the stingless bees of the subgenus *Partamona* but is applied also to *Trigona* (*Trigona*) *pallida* variety *pallida* (Latreille) and to its close relative *Trigona* (*Trigona*) *chanchamayoënsis*, new species, because of their termitophile habits. According to Peckolt (1894, p. 223) "cupira" is a corruption of the Tupi word "cupia," meaning termite. This is affirmed, too, by Silvestri (1902b, p. 143; 1903, p. 212) except that he indicates that the root word is "cupi," not "cupia." The word "cupira" thus means termite bee. This seems a more plausible derivation than that suggested by F. Smith (1863a, p. 503), who would trace the word to "curupira," meaning wood demon. In some cases, however, the name "cupira" may have been applied not because of the partiality of this bee or that for a termite nest as a place of abode but because of the resemblance of the bees' nest itself to that of a termite structure. This is particularly true of exposed nests of *Trigona* (*Partamona*) *testacea* variety *cupira* F. Smith and in the opinion of H. von Ihering (1903, p. 242) explains the name, which, he says, signifies "termite honey nest."

More peculiar on the whole than the association between bee and termite is the occupation by stingless bees of the nests of ants, for ants as a suborder have been considered among the worst enemies that stingless bees are exposed to, and the protective devices by which admission to the nests of these bees is made difficult have been interpreted as safeguards primarily against the intrusions of ants.

Allusion has been made to the occupation of subterranean nests of *Atta sexdens* by *Trigona* (*Schwarziana*) *quadripunctata* variety *bipartita* (Lepeletier) and by *Trigona* (*Paratrigona*) *lineata* variety *nuda*. But there are other cases of associations of stingless bees with ants that are even more interesting than these subsurface examples. Perhaps no nesting site reported in the case of stingless bees is quite so bizarre as that set down by Forel (1904, p. 47; 1905, pp. 170-171; 1928, vol. 1,

pp. 356-357, vol. 2, p. 282) on the basis of a discovery made by Goeldi. A nest of a small Brazilian stingless bee was noted by Goeldi in the interior of a nest of the ant *Camponotus senex* variety *textor* Forel. The nest of the ant itself is most remarkable, for its chambers, columns, and walls are made of silk secreted by the larvae of the ant. These larvae are held between the mandibles of the workers and are used as weaving implements in constructing this edifice of silk or in repairing rents in the fragile fabric.

What impelled a bee colony to establish itself in this textile dwelling? Or is it possible that the bees did not establish themselves there, but were engulfed instead by the expanding structure of the ants? Forel (1905, pp. 170-171) refrained from answering this question. "How the bees' nest came to be there—whether the ants had built around the meliponid nest or whether the meliponids had penetrated the nest of the ants—this Mr. Goeldi could not ascertain" is Forel's statement. The probability seems to me great that it is the bees that established themselves in the nest of the ants, not the ants that enmeshed in their silken galleries the structure of the bees. For bizarre as this case is in many respects, there is no good reason to suppose that it differs fundamentally from other known cases where stingless bees took up their abode in either ant or termite nests. The nest of *Camponotus senex* variety *textor* is described by Forel (1928, p. 357) as an "artistic imitation of a masonry nest or carton nest, containing countless chambers sustained by small silken pillars and connected with one another by openings." The architecture of such a nest would seem not inappropriate for a colony of stingless bees, once one has overcome the initial surprise over the venturesomeness of the bee in building combs and provision pots in such an unsubstantial house of threads. Finally it should be stated that, according to Forel, bee and ant colony "were living in peaceful parabiosis."

While the nest association discussed in the previous paragraph transcends in interest any other of which I know, it is in order to state that it is not the only reported case of a stingless bee nest found embedded in the colony of a *Camponotus* ant. Only in the instance now

to be mentioned the *Camponotus* followed the more prevalent habit of the members of its genus by establishing itself in the roomy hollow of a tree, where *Trigona* (*Trigona*) *fulviventr* variety *guianae* Cockerell decided to join it (H. von Ihering, 1903, p. 218).

A further instance of association between bee and ant, involving *Trigona* (*Scaptotrigona*) *bipunctata* Lepeletier and *Camponotus sericeiventris*, is recorded by Bertoni (1911, p. 142).

Nests of *Atta* and *Camponotus* have been mentioned as recipients of stingless bee colonies. But yet another genus of ants, *Dolichoderus*, must be credited with the role of host to a colony of stingless bees. As reported by Bequaert (1943, p. 141) this instance of association between ant and bee has unique features of interest in illustrating the interdependence of different insect groups.

"In July 1936, at Muzo, Dept. Boyaca, Colombia, I observed a voluminous nest placed in a bush some five feet above the ground. It was closely woven of a fibrous material apparently taken from some plant, not of silk secreted by larvae. When found, it harbored a thriving colony of the aggressive ant, *Dolichoderus* (*Monacis*) *bispinosus* (Olivier). The late Professor W. M. Wheeler, who named it, informed me, however, that this *Dolichoderus* is not known to weave a nest of its own, but instead usurps existing nests, particularly of termites and sometimes of other ants. He suggested that the nest found at Muzo may have been built by an *Azteca*, which was later driven from it by the *Dolichoderus*. At the time of observation part of the nest was also occupied by a colony of a small stingless bee, *Trigona* (*Paratrigona*) *opaca* Cockerell, seemingly on friendly terms with *Dolichoderus*."

A very unusual record is that reported by Lucas (1889, pp. cvii-cviii), who came into possession from Minas Gerais, Brazil, of what he interpreted as *Trigona* (*Paratrigona*) *lineata* (Lepeletier). The colony in question was obtained from the deserted pyriform nest, covered with spiny processes, of the social wasp *Myrapetra* (= *Polybia*) *scutellaris* White.

Even those stingless bees that occupy hollows in trees (and such hollows are perhaps the most popular of all nesting sites) may well be indebted in many instances to the ac-

tivities of other insects in boring away the core of the trunk or in rendering the wood soft so that the bees can remove it. Thus Ducke (1902a, p. 326) noted that various nests of *Trigona* (*Plebeia*) *goeldiana* Friese (which Ducke subsequently made a synonym of *minima* Gribodo) were discovered in the gangways bored by the larvae of beetles in old trees in the botanical garden at Pará, Brazil. Schulz (1905a, p. 200) in describing a nest of *Melipona marginata* variety *marginata* Lepeletier indicated that the hollow in which the nest was established was the work of the huge larvae of a cerambycid beetle that prior to the arrival of the bees had drilled vast passages through the iron-hard wood in obtaining their food and then after their emergence as adult beetles had flown away. Similar journeyman service had been rendered by yet other longicorn beetle larvae by way of preparing a tree hollow in which a colony of *Trigona* (*Plebeia*) *mosquito* variety *emerina* Friese set up housekeeping (Schulz, 1905a, p. 252).

The selection of the structure of some insect (termite, ant, wasp, or beetle) for the foundation of a stingless bee colony is, it would seem, very common. Of rare occurrence, on the other hand, is the establishment of a stingless bee colony in the nest of a bird.

The earliest instance of this kind that I have come upon is in Peckolt (1894, p. 91). Peckolt recorded the habit in connection with what he called "*Melipona longiceps* Smith," probably intended for *Trigona longipes* F. Smith, a synonym of *Trigona* (*Tetragona*) *varia* (Lepeletier). But the fact that Peckolt went on to describe this *Trigona* as having black hairs makes one wonder whether the insect can be *longipes*, or rather *varia*, although he heaps upon it in addition a number of popular names: "jatay de sapo," "chupé," "xupé." The popular name of *varia* is "moça branca" in Pernambuco and "abreu" in Ceará (Ducke, 1925, p. 342). The nest, however, with many reminders of its avian origin, was an interesting one, whatever one's doubts may be regarding the identity of the insect occupant. It consisted of fibers and very thin twigs and within was coated with a gum-like mass. The arched roof consisted of a more earthen material. In the floor of the nest an egg, somewhat larger than that

of the European partridge (*Perdix*), was still present but completely covered over with presumably propolis.

Salt (1929, p. 437) reported the occupation of the deserted nest of an oven bird of the family Furnariidae by a colony of *Melipona favosa* variety *favosa* (Fabricius). "The original structure had been modified by the bees to suit their occupancy."

Several instances of the use of birds' nests for the establishment of its colonies have been communicated to me in the case of *Trigona* (*Paratrigona*) *opaca* variety *pacifica* Schwarz by Dr. W. Weyrauch. Among the bumblebees a species that ordinarily favors other nest sites will now and then show a whimsical departure from its more or less orthodox behavior by taking possession of a birds' nest. What is particularly to be emphasized in the case of *pacifica* is that a birds' nest is apparently the place not occasionally but almost habitually selected by this bee as the seat of its colonies.

Before leaving the subject of birds' nests as chosen nesting sites of stingless bees, allusion should perhaps be made to an observation of Rau (1933, p. 28), who has this to say regarding a nest of stingless bees of *Trigona* subgenus *Partamona* he observed on one of the little islets in Gatun Lake, Canal Zone: "We were attracted to the nest because it looked like a bird's nest with straw on top. The straw was apparently an accident, or a bird had attempted to build on top of it, but under the straw we found a lively colony" of *Partamona*. But may this not have been another instance, like that recorded for *Trigona* (*Paratrigona*) *opaca* variety *pacifica* Schwarz, where the stingless bee gradually displaced the material of an original birds' nest by its own expanding structure until only a doubtful vestige of the original nest remained?

Places chosen as nest sites by stingless bees sometimes seem from a human standpoint to evince an amusing lack of discrimination on the part of the bees. Perhaps the oddity of their choice will be the more impressive if we confine the instances cited to a single species, *Trigona* (*Tetragona*) *jaty* F. Smith, the record of which reveals an impish perversity in converting into a nest hollow what man had intended for other ends. Williams (1928a,

(pp. 172, 173) told of a nest of this species that had been built in a letter box. Under date of March 22, 1936, Mr. G. K. Christian wrote me that at the Seminary at Pomplona, Colombia, he had been shown "a colony of these bees by Brother Constantino which were lodged in what appeared to be an oil can and the bees used the spout for an entrance." A letter, dated October 31, 1937, written me by Mr. Ferd. Nevermann from San José, Costa Rica, recorded the discovery of a nest of *jaty* in a phonograph box and of yet another nest in a sewing machine. Other colonies noted by this observer were "under the floor of a building," "in the hollow stem of *Carica papaya*," "in a fig tree," and "high up in a branch." In Panama City Dr. Charles Michener came upon a nest, regarding which he has written me, which was located in a cavity penetrated by a water line. The more or less globular mass of combs was on top of the valve in the water pipe. Dr. Anastasio Alfaro sent me an account of a nest of *jaty* that had been established in a wooden box in his home at San José, Costa Rica. Silvestri (1902b, p. 151) found *jaty* nesting in the trunks of trees and in walls, and such nesting sites are mentioned also by Marianno (1911, p. 111) and especially by Michener (1946, p. 187), who found no fewer than 28 nests in stone walls in Old Panama alone. A nest "in a small cavity at the base of a large tree" was noted by Michener at Pacora, Panama. Dr. W. Weyrauch wrote me regarding a nest observed at San Ramon, Peru, which was established in the stone wall of a house. A large wooden fence post housed a colony of this species at Guayabalito, Colon Province, Panama (Michener, 1946, p. 187). Colonies of *jaty* were observed by Wheeler (1913, p. 2) "in crevices between the buttresses or bark-ridges of large trees and between the clapboards of houses," preference being given to "the corners where the clapboards abut on the door and window frames." Bertoni (1911, p. 143) spoke of *jaty* as the species most readily domesticated and noted that it establishes itself in all sorts of hollows, even in those of stones and beneath roots, but not in the earth itself.

In spite of its wide and rather odd range of choice, as evidenced by these examples, *jaty* is said, however, to show a partiality for the tree *Hymenaea stigonocarpa* as a nest site.

Indeed H. von Ihering stated (1903, pp. 236-237) that this tree because of its association with *jaty* is known as the Jatahy tree. Von Ihering is, however, inclined to dismiss most of such claims of preference on the part of stingless bees for one tree as against another tree and leans to the belief that, where such seeming preferences manifest themselves, they are owing to the fact that the tree in question is more susceptible to decay in the heart wood than are others and hence offers better opportunity for the establishment of a nest.

While the bees themselves are disposed to occupy any suitable arboreal shelter, it has been claimed that the quality of the honey is influenced in some cases by the species of tree selected. For instance, some of the Indians of South America claim that, when the bees that they designate "aloba nate" build their nest in a tree known to the Mocobies as "abedagnic" and to the Guaraní as "ybirarira," the resulting honey is always sweeter, more agreeable, and of better taste than when the colony lodges in some other tree (Paucke, 1944, p. 256). This claim is, however, rather incredible because the honey, being sealed off in wax containers, is not exposed to contact with the wood or likely to be impregnated with its odor.

Eccentric as some of the nest sites chosen by stingless bees seem from a human standpoint, none of them exceeds the grim oddity of that recorded in the case of one of the Indo-Malayan Meliponidae, namely, *Trigona* (*Tetragona*) *canifrons* F. Smith, which selected for the foundation of its community not once but on at least two different occasions a tenantless human skull (Prell, 1919, pp. 157-162). In both instances the bees used as the point of emergence for their flight tube the empty socket of the eye, the right in one instance and the left in the other. Objects obtained for their anthropological interest sometimes inadvertently turn out to be of equal or greater entomological interest. The skulls are a case in point, but so was an amphora obtained from Peru which housed a stingless bee colony (Lucas, 1889, p. cviii).

NEST ARCHITECTURE

A nest within a hollow is commonly shut off above and below by a more or less horizontally placed partition known as a batumen

plate, which separates the inhabited portion of the cavity from the unutilized part. One or both of these partitions may, however, be absent if the cavity has a natural termination that serves the same purpose as the structures in question. Batumen plates, according to H. von Ihering (1903, p. 183), are constructed of hardened mud in nests of *Melipona* and of wax and resin in nests of *Trigona*, but the generalization is not absolute, for H. von Ihering himself subsequently (1912, pp. 44-45) came upon a nest of a *Trigona*, namely, *capitata* variety *capitata* F. Smith, in which the batumen plate was of earthen substance, while Salt (1929, p. 441) noted that the batumen plates of *capitata* variety *zexmeniae* Cockerell were "of hard and brittle cerumen containing much earth."

The nest is often made conspicuous by the flight hole, which in nests of *Trigona* is frequently, and in nests of *Lestrimelitta* possibly always, expanded externally in the form of a cylinder, spout, tube, or trumpet, sometimes extending outward as much as 35 centimeters—that of *Lestrimelitta limão* (F. Smith) according to Bertoni (1911, p. 141)—and variable in diameter. In contrast to this elaboration of the vestibule of the nest, other *Trigona* may have only a small protective ring about the entrance or even no ornamentation whatever, just an unadorned hole. Sometimes the flight tubes are multiple, and have earned for a species like *Trigona (Scaptotrigona) postica* Latreille the popular name in Brazil of "sete portas," according to Ducke (1916, opposite p. 28; 1925, p. 343), although according to H. von Ihering (1903, p. 222), this name is presumably applied to *Trigona (Tetragona) jaty* F. Smith. Eccentric flight holes of *iheringi*, which has been interpreted as close to *postica* (Ducke, 1916, p. 112; 1925, p. 405), and of *jaty* are shown respectively on plate 6, figure 1, and plate 4, figure 1.

Rau (1933, fig. 1) reproduced a photograph taken on Barro Colorado Island, Canal Zone, showing two rather closely placed entrance portals built by a variety very closely related to *Trigona (Partamona) testacea* variety *cupira* F. Smith. The separating space between the portals, although not great, might have suggested the presence of two nests, and indeed this was Rau's conclusion until he explored the architecture and found that

both portals led to the same destination. Rau decided to put to the test the building enterprise of this colony, so he plugged both the openings with cotton, whereupon four other openings "were soon made elsewhere on the spout" (Rau, 1933, p. 18). Not only in the New World but also in the Old stingless bees occasionally indulge in such architectural exuberance. Thus Karawaew (1905, pp. 10-11, pl. 2, figs. 15, 16) recorded a nest of *Trigona (Tetragona) apicalis* F. Smith from the island of Singapore that had two very similar trumpet-like entrances placed the one immediately next to the other a couple of feet above the surface of the ground in a tree trunk.

In nests of *Lestrimelitta limão* (F. Smith) there are stalactite-like outgrowths or knotty protuberances (pl. 3) that are more or less clustered, especially on the under side of the flight tube, giving this flight tube a rough and uneven appearance. In nests of *Trigona*, however, the projecting tube is usually rather smooth and symmetrical, and with usually only a single orifice.

It was the conclusion of Benton (1894, p. 23) that "propolis is doubtless the material of the tubes," thus taking issue with Girard (1874b, p. cvi; 1874c, p. cxi) that the vestibule to the nest is of waxen consistency. However, H. von Ihering (1903, p. 240) referred to the flight tubes of *Trigona* as in most instances waxen, while Rau (1933, p. 32) described the flight tube of *Lestrimelitta limão* (F. Smith), by some still regarded as a subgenus of *Trigona*, as consisting of "a blackish mixture of wax and other substances." It would seem even from these few cited cases that it is unsafe to generalize regarding the materials that enter into the composition of the portal of the nest. Indeed H. von Ihering himself (1903, p. 240) indicated that the entrance to the nest of *Trigona (Scaptotrigona) bipunctata* (Lepeletier) consists of brittle dark cerumen, while the nest of what he interpreted as *Trigona (Partamona) testacea* variety *cupira* F. Smith is built of mud and resembles the mouth of a frog. Furthermore H. von Ihering went on to say that in the case of ground-nesting *Trigona* such as *basalis* [which is a synonym of *Trigona (Schwarziana) quadripunctata* variety *bipartita* (Lepeletier)] the entrance tunnel is occasionally lengthened outwardly into a thin-walled tube of mud.

When we come to the genus *Melipona*, the employment of earthen materials in constructing the approaches to the nest is the general rule rather than the exception. Often in this genus the flight hole is the center from which radiate a number of ridges or raised ribs that give to nests of, for instance, *Melipona quadrifasciata* variety *anthidioides* Lepeletier (pl. 2, fig. 1) and certain other representatives of the genus, a rather distinctive appearance. Dr. C. D. Michener, in a letter addressed to me, expressed the suspicion that the material used by *Melipona favosa* variety *phenax* Cockerell for the external part of its habitation "comes from old termite nests." His observation was made in Panama.

It is sometimes possible from the exposed part of the nest to recognize the occupant. But not always is the handiwork distinctive and not always is the architecture of the entrance constant and dependable. The nest may occasionally be devoid of ornament in the way of a tube or spout even in the case of species that ordinarily build such external structures.

It is the contention of Jacob (1932, p. 150) that the age of a nest may be gauged by the length, solidity, and color of the flight tube. "In old dwellings," stated this author, "it is long, slanting, black and thick. In the case of young settlements the tubes are shorter, the color light, and the wall porous." However, this test would seem to be far from infallible. In view of the age of some stingless bee nests that endure from year to year, accidents to the tube that require replacements may be assumed to be a not unusual occurrence. In the case of *Lestrimelitta limão* (F. Smith), at least, we know that replacements occur from time to time (Holmberg, 1887, pp. 284-285). Thus a new tube may become associated with an old nest, and, losing its freshness of appearance, may even be mistaken for the old tube.

The speed with which a new tube is constructed when the old tube is forcibly removed is always a cause for astonishment. Rau (1933, p. 33) after removing the spout of *limão* was surprised, when two days later he revisited the nest, to find "that in that short interval these ambitious little creatures had made a new entrance tube extending out

several inches from the trunk." Similarly when on Barro Colorado Island I revisited a nest of *Trigona* (*Scaptotrigona*) *pectoralis* Dalla Torre at nine o'clock on the morning of March 24, 1933, I was interested to find that a new flight tube had been very nearly built up to the size of that removed in the forenoon of the previous day. The tube was paper thin, shaped a little like a morning-glory, with the orifice wider than the base. The depth of the tube originally was, I would judge, about 3 inches and its approximately circular outer edge had a diameter estimated to be 2 inches.

L. E. Cheesman (1933, p. 58), too, has contributed an interesting observation regarding the industry of stingless bees in repairing the portal of their nest. The species was one that she took with her from the tropics and succeeded in establishing in England, where it survived for more than a year. The projecting spout of the nest, as depicted in her drawing (p. 55), would seem to have been of substantial length and in fashioning it the bees kept up their activities "the whole of the day and far into the night," and, adds the author, "probably all night long, for when I saw them early next morning they were still working, and they continued until late that afternoon."

With such impressive demonstrations of industry it is not surprising that the finished results are so soon achieved. However, an instance to the contrary is that cited by Michener (1946, p. 189) in which the entrance tube that replaced a tube removed from a nest of *Trigona* (*Trigona*) *fulviventrís* Guérin required six weeks to achieve the stature of its predecessor.

Before continuing with a description of the nest architecture it seems appropriate to mention yet another instance, cited by Wheeler (1913, pp. 4-5), of the alacrity of stingless bees in making needed repairs. With the points of his tweezers Wheeler tore away the diaphragm of pale yellow wax that closed the crack in a wooden pillar in which was located a small colony identified as *Trigona* (*Plebeia*) *frontalis* Friese. The bees set to work reconstructing the broken part from within, and in 20 minutes had restored the diaphragm. Again and again Wheeler put the bees to the test and in each case they met

the challenge indefatigably, accepting their labor of Sisyphus with monotonous submissiveness. "Finally," stated Wheeler, "after spending some hours in this destructive employment, my patience was exhausted and I left the little creatures to enjoy their harmless and unobtrusive existence." It is time that we, too, leave our contemplation of the external features of the hive and follow the bees into the interior.

Extending inward from the flight hole is a tunnel-like or tube-like passageway that conducts to the brood chambers, usually located in the central part of the nest. Here the cells are arranged as a rule in combs that, unlike the combs of the honeybee, are placed not vertically but horizontally, and, again unlike the standard of the honeybee, consist of a single layer of cells only, all of which face upward, not, as in the honeybee, of two layers of cells placed base to base and facing in opposite directions, right and left. The brood combs of stingless bees are, in other words, placed each as a tier or story one above the other. Between the combs, giving support to the structure and keeping each story separated from the other, are, as a rule, pillars of wax. Usually such pillars extend only between two neighboring combs, but in some cases they penetrate several successive combs, forming a continuous structural element. In nests of *Trigona* (*Trigona*) *fulviventris* variety *guianae* Cockerell observed by H. von Ihering (1903, pp. 217-218, 247) such a prolongation of the supporting elements was noted sometimes over eight to 10 combs and not only near the rim of the combs but also inward. In most cases these supports terminated dichotomously. Rau (1933, p. 21) in describing a nest built by a member of *Trigona* subgenus *Partamona* stated: "There are occasional small props or pedicels between the horizontal combs, but the main reinforcement is a series of vertical pillars, one-eighth inch thick, going from the floor to the top of the nest, passing directly up through the many combs."

In addition to supporting elements between combs, there are often also openings (due to missing cells) within each comb, which serve as passageways for the bees and possibly also for ventilation. Schulz (1904b, p. 819) noted in a nest of *Melipona fasciata*

variety *scutellaris* Latreille that such openings might be consecutive over as many as three combs or tiers.

While the horizontal position of the successive combs is the usual one, there are instances when the arrangement is oblique. Thus H. von Ihering (1903, p. 224) recorded a nest of *Trigona* (*Plebeia*) *molesta* (Puls) in which the brood combs lay in the direction of the length of the trunk, "possibly forced into this orientation by the fact that the trunk had not stood perpendicularly but at an incline." The impression that dislocation in the arrangement of the combs is owing to the divergence from the perpendicular in the growth of the tree or of that part of the tree that contains the nest receives confirmation from those nests that are located in fallen trees or that have been removed from their arboreal anchorage. Thus H. Müller (1874, p. 32) told of a nest of *Trigona* (*Oxytrigona*) *tataira* variety *tataira* F. Smith that was found by his brother, "in a tree cut down a long time before." Its combs were "lying in confusion, probably in consequence of the direction of the trunk having been altered by felling the tree." But the most convincing case of this character is that cited by Lutz (1924b, p. 507) regarding a *Trigona* nest that, originally in the branch of a tree, had been cut down with the branch:

"Although the nest was lying sideways on the ground, the bees were still using it after having made certain interesting alterations. These nests had been made by ants but the ants had moved out and the bees had moved in. Curiously enough, the entrance which the bees make in the interior of the nest is on top and funnel-shaped as though designed to catch the rain, and this seems foolish.¹ The brood cells are arranged in horizontal layers within. Now, the nest which had fallen and was lying on its side had two entrance holes: the old one, which was on what had been the top of the nest, and a new one, which was on

¹ Although the species of *Trigona* that built with such eccentric disregard of the rainy conditions in the Canal Zone is not mentioned by Lutz, it is pertinent to state that among the 52 nests of *Trigona* (*Nannotrigona*) *testaceicornis* variety *perilampoides* Cresson examined by Michener, there was one that had the entrance tube "projecting straight upward from the top of the wall instead of horizontally from the side as usual" (Michener, 1946, p. 185).

what was subsequently the top. Furthermore [and this is the passage of particular bearing upon the present discussion], when the nest was opened, it was found that the layers of brood cells were in two planes: one the old horizontal and the other the new."

A nest of *Melipona beecheii* variety *beecheii* Bennett figured by E. T. Bennett (1831, pl. between pp. 358-359) also shows departures from the normal in the placing of the combs, some being horizontal, others vertical. This nest had been shipped from Mexico to England, where, deposited in the Linnean Society, it was cross sectioned longitudinally so as to reveal the interior. One infers from the atypical arrangement of the combs that the log which enshrined this nest had been at one stage vertical in position and subsequently had been placed in a horizontal position, thus compelling the bees to change the direction of their comb structure to correspond with the shift of 90°.

Such departures from the normally uniform orientation of the successive combs would seem to be due to exceptional circumstances, accidents that change the direction of the main axis of the nest or the like. An even more interesting modification of the architecture of the brood chamber occurs when the combs form a broad spiral that extends upward in one unbroken helix. While the horizontal, more or less detached arrangement of the combs is the more usual one, the spiral staircase type of continuous comb has been noted in nests of Latreille's *ruficrus* (H. von Ihering, 1903, p. 230) and Olivier's *amalihea* (Salt, 1929, p. 439) of the subgenus *Trigona*, in Lepeletier's *quadripunctata* (H. von Ihering, 1903, p. 228) of the subgenus *Schwarziana*, and in a nest of a member (incorrectly referred to as *dorsalis*) of the subgenus *Scaptotrigona* (H. von Ihering, 1903, p. 213). Subsequently H. von Ihering (1912, pp. 43-44) described yet another nest of mainly spiral staircase type constructed by yet another *Scaptotrigona*, either *postica* Latreille (identification of Friese) or *bipunctata* Lepeletier (identification of Schrottky). The spiral staircase type of nest was recorded by Hockings (1884, p. 150) in the case of an Australian *Trigona* known as "karbi" or "keelar" that he believed to be *carbonaria* F. Smith. This type of nest architecture

occurs, therefore, in both the Old and the New Worlds. This method of building is possibly only a somewhat flexible variant from the common type, for in some nests that have been observed—those of *Trigona* (*Trigona*) *corvina* Cockerell and of *Trigona* (*Oxytrigona*) *tataira* variety *mellicolor* Packard—the combs of the lower part of the brood chamber are horizontal in position while the top group of combs contrasts with these in being spiral in arrangement. I am indebted to Mr. F. Nevermann for communicating to me cases of this hybrid type which he observed in the two species noted.

The brood chamber of the majority of the nests of *Trigona* in most of its subgenera and also of *Melipona* conforms either to the successive superimposed horizontal tier type of architecture or to the spiral staircase type, with the latter probably merely a modification of the former. But there is yet another type of brood chamber that is wholly different from either. This is the so-called cluster type of cell arrangement. In nests of this type the cells are not arranged in horizontal combs or in a continuous stretch of closely placed units forming a story. Instead, the cells are irregularly clustered, often without orientation, and separated by minute intervening pillars of wax. Drory (1873c, p. 173) was seemingly the first to describe a nest of this character and cited the opinion of Brunet regarding a stingless bee [probably *Trigona* (*Tetragona*) *nigra* variety *paupera* (Provancher)] that likewise built cells of the cluster type.

"Mr. Brunet believes that, in view of their peculiar manner of constructing their nest, as well as the fact that there are living simultaneously in the same colonies individuals of two different types of coloration (namely, those of white abdomen and those of dark abdomen), this species can be neither a *Melipona* nor a *Trigona*, as all the members of this family surround the true brood chamber with a more or less deftly made, mysterious, labyrinthine envelope. I agree with him."

Another early reference to this type of nest structure was made by Girard (1875a, p. 572; 1879, p. 725) in the case of what he designated as "*Trigona cilipes*," although *cilipes* is a Fabrician species originally de-

scribed as a *Centris* (Fabricius, 1804, p. 361) and difficult to place with confidence. From Girard's description it would seem that possibly he interpreted as "*cilipes*" the species *Trigona* (*Tetragona*) *nigra* variety *paupera* (Provancher) above referred to.

Subsequently H. von Ihering (1912, pp. 1-5) noted this type of nest structure in the case of *Trigona* (*Tetragona*) *silvestrii* Friese, and it impressed him as so distinctive that he made this stingless bee the type species of a new genus, *Friseomelitta*. It is gravely open to question, however, whether, in spite of the reasoning of Brunet, Drory, and Friese, such a genus based on nest architecture is justified. Morphologically *silvestrii* is assignable to the subgenus *Tetragona*, and the cluster type of brood chamber that H. von Ihering believed so distinctive is shared, according to subsequent observations, by several species belonging to other subgenera of *Trigona*. Among the New World stingless bees that build this type of nest Ducke (1916, p. 25; 1925, p. 340) enumerated, partly on the prior published records of H. von Ihering: *duckei* Friese and *muelleri* Friese (H. von Ihering, 1911, pp. 129-136), of the subgenus *Hypotrigona*; *silvestrii* Friese (H. von Ihering, 1912, pp. 1-5) and *varia* (Lepelletier), of the subgenus *Tetragona*; *minima* Gribodo, of the subgenus *Plebeia*; and *timida* Silvestri and *schrottkyi* Friese, of somewhat doubtful affiliation. Later, Salt (1929, p. 443) found that yet another bee, *Trigona* (*Tetragona*) *nigra* variety *paupera* (Provancher)¹ (possibly the "*cilipes*" of Girard) builds likewise in this general manner, "the cells not being arranged in tiers but like yellow beads strung irregularly on a network of cerumen fibres." Finally Wheeler mentioned (1923, p. 128) an undescribed species allied to *goeldiana* (considered by Ducke a synonym of *minima* Gribodo) whose nest conformed to this general architectural pattern. It was the contention of Bertoni (1918,

p. 224) that the nest of *Trigona* (*Plebeia*) *minima* Gribodo was perhaps more primitive than certain other nests within the cluster type, but Bertoni's brief description does not sufficiently indicate the bases of his belief.

To Old World stingless bees that have their brood cells arranged not in combs but in clusters after the manner just indicated belong the "kootchar" of Australia (Hockings, 1884, p. 152), which was subsequently described by Cockerell (1929a, p. 299) as *Trigona cassiae*. As builders of this type, too, Schulz designated *laeviceps* F. Smith (1907, pp. 65-73) and *canifrons* F. Smith (1909, pp. 338-341). It is likely, however, that both of these reported instances should be referred to *Trigona* (*Tetragona*) *iridipennis* F. Smith (Friese, 1914a, p. 44; Schwarz, 1939c, pp. 88-89, 111-116). Prell (1919, pp. 157-162) also mentioned *canifrons* F. Smith as a bee that builds its brood cells in clusters, not in combs, but whether Prell's *canifrons*, like that of Schulz, is to be referred to *iridipennis* I cannot say. That *iridipennis* indubitably builds its brood cells in clusters is substantiated by a field note made by W. G. Van Name in the Philippines regarding a colony that is certainly *iridipennis*. "These little bees," Van Name noted, "built grapelike cells forming an irregular mass 6 by 4 inches in the drawer of a table. Some much longer cells [doubtless the provision cells] in separate group. Wax tunnel also built in drawer" (Schwarz, 1939c, p. 113).

To the group of Old World cluster builders belong also a bee that Waterhouse (1903, pp. 133-136, pl. 6) referred to as *Trigona collina* F. Smith, but which more probably was typical *apicalis* F. Smith (Schwarz, 1939c, p. 126), and a bee that he determined as *Trigona ruficornis* F. Smith (now *smithii* Bingham).

Not only are the absence of combs and a cluster-like arrangement of the brood cells differentiating characteristics of nests of the primitive type just discussed, these species also show in their nest architecture yet another departure from the more orthodox building methods of stingless bees generally in that they lack the so-called involucrum that is a common structural feature in the vast majority of meliponid nests.

One possible exception to this generaliza-

¹ Originally Salt's insect was recorded as *Trigona nigra* Cresson, variety *parastigma* Cockerell. At the time I made this identification for Salt I had not yet had an opportunity of examining Provancher's types in the Public Museum in Quebec. Provancher's *paupera* proves to be the same insect that Cockerell (1918a, p. 165) described as *parastigma*, and *paupera* accordingly has priority.

tion should perhaps be noted before proceeding to an account of involucra in detail. It concerns the Australian stingless bee known as the "kootchar" (*Trigona cassiae* Cockerell). The brood cells of this bee, as described by Hockings (1884, pp. 152-153), are globular and "placed in a conical heap on the top of one another, without any regularity." The description clearly indicates that the arrangement of the cells is of the cluster, not of the comb, type, and, as such, they should lack an envelope. Yet Hockings stated in the next breath that "as in the other variety, they are encased in a sheet of wax to economise the heat necessary for the maturity of the young." The "other variety" with which comparison is drawn is *Trigona carbonaria* F. Smith, a species that builds its brood cells not in clusters but in combs (sometimes spirally arranged). The allusion by Hockings to the envelopment of the brood chamber in these two species (*cassiae* and *carbonaria*) is worthy of emphasis, tending as it does to raise the question whether or not the absence of an involucrum is always to be associated with nests of the cluster type of brood cell aggregates. "Sheet of wax" is, however, a very inadequate term with which to describe the complexity of the involucrum constructed by those stingless bees that fashion an involucrum, and perhaps, therefore, no involucrum as it is ordinarily conceived was involved.

The involucrum is an envelope that encloses the entire brood mass in those nests in which the brood cells are arranged in combs, being connected with these often by pillars of wax. Frequently the involucrum consists of fine wax lamellae irregularly connected with one another. In nests of *Melipona*, according to H. von Ihering (1903, p. 242), these lamellae are arranged in only two or three concentric layers but in nests of *Trigona*, according to the same authority, there are not infrequently 10 or more such layers. Often these lamellae are soft and pliable, but sometimes (particularly in nests that are exposed instead of concealed within a hollow) they are hard and fragile and to such aggregates of hard lamellae H. von Ihering gave the name *spongiosa*. The irregular passageways that communicate with one another within this labyrinthine com-

plexity constitute a resting place for the bees. The involucrum doubtless also is a barrier against enemies of the bees and serves likewise for the retention of the heat within the brood chamber. In an exposed nest of the genus *Partamona* that Rau (1933, pp. 17-19) examined on Barro Colorado Island, Canal Zone, the "hard exoskeleton or shell of the nest" (the portion corresponding to H. von Ihering's *spongiosa*) was "covered with a layer of dirty varicolored material which is easily crumbled." In exposed nests, it may be noted, the protective envelope encloses not only the brood chamber but the provision pots as well, and this is also frequently the condition in nests that are not exposed, but in other instances the provision containers are outside the involucrum.

Not always is the *spongiosa* made of an admixture of earth with cerumen. The envelope of a nest of *Trigona* (*Trigona*) *trinidadensis* variety *trinidadensis* (Provancher) reported by Weyrauch (1942, pp. 62-64) from Peru consisted of only a thin wall of wax immediately surrounding the brood and provision jars, followed outwardly, however, by several concentric layers of a paste consisting of macerated leaves, each successive layer fitting into the contours of the preceding one. Further cohesion was secured by a number of tiny wax pillars placed at irregular intervals in each layer. A second nest observed by Weyrauch also had the envelope composed largely of chewed leaf particles although intermixed with an abundance of black and very sticky resin.

The outer envelope of the nest of *Trigona* (*Trigona*) *ruficrus* (Latreille) consists, according to Silvestri (1902b, pp. 136-137), of from six to 10 concentric layers, produced in large part from the dung of herbivorous animals. But according to Marianno (1911, p. 127) it is not the dung in its entirety that is used but merely the undigested particles of vegetable matter, which are removed by the bee, with the aid of its mandibles and fore legs. This observation seems to point to the possibility that *trinidadensis*, or an ancestral form, may at one time have obtained its leaf fragments in similar fashion or that *ruficrus* may have originally foraged among the trees for its building material instead of following the cow paths, or that any source

of supply will be exploited. The significant point is that both of these species (belonging to the same subgenus) employ leaf material in the envelope of the nest.

A weighty, rounded to bowl-shaped mass of earthen material mixed with wax and resin (pl. 6, fig. 4) is found in the nests of *Trigona* (*Trigona*) *ruficrus* (Latreille) beyond the brood chamber and the provision pots. This structure, upon which H. von Ihering has bestowed the name of scutellum, may occupy more than one-half of the entire nest (H. von Ihering, 1903, p. 230, pl. 21; Dücke, 1925, p. 418) and adds greatly to its weight. The scutellum is essentially solid but penetrated here and there by irregular passageways, which are sometimes completely filled with the bodies of dead bees (H. von Ihering, 1903, p. 229). Bertoni (1911, p. 143) implied that such an earthen disk is found also in nests of *Trigona* (*Cephalotrigona*) *capitata* variety *capitata* F. Smith and *Trigona* (*Trigona*) *amalthaea* (Olivier).

Among the oddities that have been noted in the nests of stingless bees may be mentioned hard coin-like disks, slightly convex on one side, slightly concave on the other, and made of resin with admixture of sand. Such disks were discovered attached to the lamellae of the involucre in a small nest of *Melipona marginata* Lepeletier (Schulz, 1905a, p. 203). These penny-like pieces bore snail-like windings sculptured on their concave side.

A still more mystifying structure, noted also by Schulz (1905c, p. 142), was a little vessel of a mixture of resin and sand that Schulz saw a small black *Trigona* species placing in numbers on the bark of large trees. To add to the bewilderment these gall-like structures often contained eggs and small larvae. The observation as yet defies interpretation. If *Trigona* and resin were not mentioned, one would be tempted to think that the structures were perhaps the work of eumenid wasps.

Caches of resinous material have been reported from stingless bee nests. Usually these are of ordinary type, but Wheeler (1923, p. 128) recorded that in a nest of black *Trigona* at Kalacoon in British Guiana, were "several lumps, each weighing 10 to 20 grams, of a hard substance closely resembling

sealing wax in color and consistency." This comment recalls the statement of F. Poey (1852, p. 158) to the effect that a trusted friend of his had frequently observed in nests of *Melipona beecheyi* variety *fulvipes* Guérin large pieces of a vitreous substance resembling sealing wax, while others, half worked over by the bees, were paler and more sticky. Very possibly this "sealing wax" is a red resin, for F. Müller (1875, p. 296) noted that in southern Brazil stingless bees were partial to the sap resembling dragons' blood that flows from the blood tree (*Pterocarpus*) and that this resin imparted a brownish red or reddish color to the wax. The resin of stingless bees is usually deposited freely but sometimes apparently it is stored in special containers. Silvestri (1902b, pl. 3, fig. 42) found this condition in a nest of *Trigona* (*Tetragona*) *mombuca* variety *subterranea* Friese.

Unlike the condition in the colonies of the honeybee, the honey and pollen of stingless bees are not stored in combs but are placed in jars that are more or less globular, oval, or at times cylindrical. The last-mentioned condition was found to be the case in pollen jars in a nest of *Trigona* (*Tetragona*) *silvestrii* Friese (Silvestri, 1902b, fig. 13c; von Buttel-Reepen, 1903a, fig. 14a). The jars, whether their contents be honey or pollen, tend to be in clusters or groups, so that the wall of one jar may be contiguous to the wall of another jar or connected with it by short pillars of wax. The interconnected receptacles thus often constitute a rather compact unit with comparatively little free space and may often be lifted as one mass.

As far back presumably as 1774, when the first edition of Oliver Goldsmith's "History of the earth and animated nature" made its appearance, this compactness of the provision jars was recognized. At any rate, in a later edition (1824, p. 146) of this work it is stated that the stingless bees "lay up their honey in waxen vessels, of the size of a pigeon's egg, of a black or deep violet colour; and these are so joined together, that there is no space left between them." Almost the identical language is employed by an anonymous writer (1792, p. 119) of the late eighteenth century, who adds, however, the unusual if not very helpful comparison that the jars are

"in the shape of air-bladders of carps." Thus the nest interior of these bees was awakening interest at a period when awareness of nature had not yet been fully alerted. Indeed, at the time that the first edition of Goldsmith's work was published, no stingless bee had as yet been described and 15 years were to transpire before Olivier (1789, pp. 78-79) established a toe-hold in science for this large group by setting down the characters of *amalihea*. With too great a show of caution, however, Olivier assigned it to *Apis* instead of giving it generic independence.

Ordinarily the jars are located both above and below the brood chamber, but sometimes they are all concentrated above, and in other instances they occur only below the area occupied by the brood. According to the observations of F. Müller (1875, p. 295), the distribution of the provision containers tends to be governed by the position of the nest entrance. If the nest entrance is near the middle of the nest, the top and the bottom of the nest are apt to have such containers. If the nest entrance is towards the top of the nest, the containers will be found towards the bottom of the nest, and at the top if the nest entrance is towards the bottom. Not always, however, are the containers placed only above or below the brood chamber. There are cases where, in addition to being above and below, they extend also more or less along the side. Sometimes indeed the arrangement of the food receptacles may be wholly lateral, forming a fragmentary or more or less complete girdle or ring about the combs. Such a condition is reported by H. von Ihering (1903, pp. 227-228) for *Trigona* (*Schwarziana*) *quadripunctata* variety *quadripunctata* (Lepeletier). In the domesticated colonies of *Melipona beecheii* Bennett the honey pots were at the lateral extremities, a building modification due doubtless to the horizontal position of the hollowed log intended for the reception of the bees. According to E. T. Bennett (1831, pp. 357-365), this log, plugged at each end, was robbed of its honey through the simple act of removing the plug and seizing the adjacent honey pots.

The number of provision containers may run to impressive totals, especially in nests of species that fashion containers of small circumference but that have large populations

to support. In a nest of *Trigona* (*Tetragona*) *jaty* F. Smith there were, according to Salzedo, more than 200 jars (cited by Raveret-Wattel, 1875, p. 743). In the lower part of a nest of *Trigona* (*Trigona*) *amalihea* (Olivier) were "several hundreds" of pollen pots, although—strange disparity—not more than 10 or 12 honey pots (Salt, 1929, pp. 438-441). Above were honey pots but few pollen pots. Such inequalities in the representation of pollen pots and honey pots are not altogether unusual. F. Poey years ago (1852, p. 157) commented on a nest of *Melipona beecheii* variety *fulvipes* Guérin that had a considerable number of pollen pots but only two devoted to honey. The disproportion may favor the pollen pots in some cases, the honey pots in others. We have just cited Poey with reference to the preponderance of pollen pots in a nest of *fulvipes*. In a nest of *Trigona* (*Cephalotrigona*) *capitata* variety *zexmeniae* Cockerell examined by Salt (1929, pp. 441-442) the situation was reversed: there were only four pollen pots in the entire nest in contrast to the numerous honey pots. More extreme than this condition, with the pendulum swing back in the opposite direction, is the nest of *Trigona* (*Schwarziana*) *quadripunctata* variety *quadripunctata* (Lepeletier) observed by H. von Ihering (1903, p. 228) in which the containers were "all filled with pollen, not one of them held honey." Doubtless H. von Ihering is justified in his conclusion that this one-sided condition of things may well be different at other times of the year. Indeed, it was the observation of Brunet that in Bahia, Brazil, the stingless bees gathered honey primarily in summer, on which they lived subsequently when summer came to an end in March and April, whereas pollen collecting was the principal outdoor activity when they were not foraging for honey (cited by Raveret-Wattel, 1875, p. 755). On the other hand, Rayment (1932a, p. 251; 1935, p. 535) concluded from his observations that *Trigona* colonies in which there was great plenty of pollen "but not one drop of honey" would dwindle away.

The honey pots and pollen pots are sometimes indistinguishable; in other cases they differ not only in size but sometimes even in shape. Of very contrasted shape and size were those figured by Silvestri (1902b, figs.

14a, 14b) from a nest of *Trigona* (*Tetragona*) *silvestrii* Friese, one of the builders of cluster-type brood cells. In this case the honey pots were of only moderate size and oval; the pollen pots, on the other hand, were large, elongate, and cylindrical. As pointed out by von Buttel-Reepen (1903a, p. 132), this disparity of structure finds its parallel in the type of provision containers fashioned by some of the bumblebees—he mentioned *Bombus pomorum* (Panzer)—in which cylinders are reserved for pollen, rounded pots for honey. An extreme disparity of size is reported by Morstatt (1921, p. 289) in connection with a nest of the African *Trigona clypeata* Friese, in which the pollen pots had a content three or four times that of the honey or the brood cells.

The size of the brood cells tends to approximate the size of the occupant, and is thus variable according to the species involved. In respect to the food jars there is considerable disparity of size. The largest containers that came to the notice of H. von Ihering (1903, pp. 200, 201, 244) were those in a nest of *Melipona schencki* Gribodo (listed by H. von Ihering as *Melipona nigra* Lepeletier). One of these containers measured 55 by 48 mm. with volume of 28 ccm., and held 32.5 grams of pollen. "For purposes of comparison," stated H. von Ihering, "a fairly large hen's egg 53×38 mm. has a content of 37 ccm. A hen's egg 53×43 mm. has a volume of 46 ccm. The size of the egg last referred to is almost the same as that of the above-mentioned provision jar of *Melipona nigra*, but the egg has a very much greater content due partly to the irregular shape of the *Melipona* container but mainly to the excessively thick walls with which it is enclosed."

Hardly less impressive is the size of the food jars recorded for *Trigona* (*Cephalotrigona*) *capitata* F. Smith. In the case of typical *capitata*, jars measuring up to 52 mm. by 40 mm. have been reported (H. von Ihering, 1912, pp. 44–45). For *Trigona* (*Cephalotrigona*) *capitata* variety *sexmeniae* Cockerell jars of somewhat smaller size, 35 mm. to 40 mm. in length by 25 mm. in diameter, are indicated (Salt, 1929, p. 441).

The jars of *capitata* are reported by both H. von Ihering and by Salt to be thin walled, thus assuring more space for the honey and the pollen. In contrast *Melipona mondury*

F. Smith, which is hardly to be separated from *Melipona fasciata* variety *rufiventris* (Lepeletier), builds provision containers with walls ranging from 4 to 10 mm., in places even 18 mm. (H. Müller, 1875b, p. 45). Walls of such excessive thickness as those just mentioned, indicating an exceedingly wasteful use of building material, must be regarded as exceptional. In general the thickness of the walls of the provision containers is, in the case of *Trigona* nests, that of writing paper; in the case of *Melipona* nests, that of leather. Within a given species, however, and even within a given nest disparities of thickness occur. H. von Ihering (1903, p. 244) explained these disparities by stating that "containers in new, recently constructed nests and also such containers in older nests as are obviously constructed freshly of new wax, always have thin walls."

It is *capitata* that among *Trigona* seems to have the largest provision containers, approximating in this respect the larger members of *Melipona*. In contrast, other *Trigona*, for instance, *schrottkyi* Friese, have honey containers no larger than 5 to 7 mm. While figures are not available regarding the size of the provision jars in nests of the tiny *Trigona* (*Hypotrigona*) *duckei* Friese, it is probable that the jars of that species, as well as of some of the other small *Trigona* bees, are even more diminutive than those cited for *schrottkyi*. Jars of progressively larger size, more or less filling the gap between these extremes, might be cited for other species.

The populations of nests may vary considerably. In the case of the species just mentioned, *schrottkyi*, H. von Ihering (1903, p. 232) estimated that the number of individuals in a nest he opened could hardly have exceeded 300. In contrast to a small nest of this sort the same author (1903, p. 215) estimated the population of a nest of what he designated *dorsalis* [but what is probably to be interpreted as close to *Trigona* (*Scaptotrigona*) *postica* Latreille] to be between 70,000 and 80,000 adults. This figure compares favorably with that for large colonies of our honeybee. It should be emphasized, however, that H. von Ihering's total was an estimate and not an actual count, and was based on the impression, derived from an examination of another nest of the same spe-

cies, that the number of adult bees exceeded the number of cells in the nest. The cells H. von Ihering estimated as being in excess of 64,000.

The nest containing this large population consisted of 27 combs. But in a nest of the same species (p. 214) with fewer adult individuals (by count 24,423) there were no fewer than 40 combs, including small and incomplete ones. The combs in this instance had far fewer cells per comb than was the case in the nest of 27 combs, and hence the aggregate of cells was smaller even though the number of combs was greater. Among the large nests recorded must be mentioned also that of *Trigona (Trigona) amalihea* (Olivier) observed by Salt (1929, p. 439) which had 35 tiers of cells and an aggregate of cells estimated as "at least 20,000."

It is very easy to rattle off figures without reflecting on their meaning. True, the total compass of an edifice erected by stingless bees is not great but, compared to the size of the builders, it is an imposing structure. Our Empire State Building with its 102 stories has tended to dwarf the Woolworth Building with its mere 60 stories. And yet it was not so long ago that the Woolworth Building captivated the imagination as the most aspiring accomplishment of man's effort to penetrate architecturally the high reaches of the sky. Even 40 stories, as recorded for a stingless bee, is, therefore, not to be dismissed as insignificant notwithstanding the fact that this triumph of the insects' building art is concealed from view in a tree hollow.

Populations of *Trigona* may present startling contrasts from species to species. Citation has been made of H. von Ihering's estimate of 80,000 adult members in the nest of one species contrasted with merely 300 in the nest of another. Even the 300 adults reported by von Ihering for *schrottkyi* seem, however, a relatively large total when compared to the diminutive nest populations mentioned by Bertoni (1918, p. 224) in the case of *Trigona (Plebeia) minima* Gribodo, which in some colonies has a representation of no more than a few dozen individuals. Wheeler, too, indicated (1913, pp. 4-5) that another *Plebeia*, namely, *frontalis* Friese, in Guatemala has colonies limited to a few dozen workers.

Melipona nests commonly show no such stupendous differences in the census of the occupants, although their populations may range from a very few hundred to a few thousand. One of the most populous nests reported for *Melipona* was a nest of *Melipona fasciata* variety *rufiventris* Lepeletier, consisting of 15 combs and containing, according to the calculations of H. von Ihering (1903, p. 202), about 7000 immature bees. The adult population of this nest may not have been less than 7000.

Yet it is possible that some of the estimates made in the past, which were not based on an actual count, individual by individual, of the nest population, were excessive. At any rate, some very large nests house populations which do not correspond with one's expectations. Thus the recovered population of a nest of *Trigona (Trigona) corvina* Cockerell that C. D. Michener collected at Juan Mina, Canal Zone, on April 27, 1945, consisted of 6529 specimens, which, according to his estimate in a letter to me, was more than 90 per cent of the entire colony. Yet the nest itself was an unusually large one, for it weighed 69 pounds. However, Michener estimated (1946, p. 194) that there were 82,000 brood cells, thus indicating a potential population many times that of the actual population when the nest was examined.

BUILDING TECHNIQUE

A survey has been given of the architectural plan of the nests of stingless bees but how does the work of construction actually proceed? The social wasps begin at the ceiling, as it were, suspending one story below another, all ultimately supported by the prop or anchorage at the roof. The cells that constitute these successive stories or combs all face downward. The condition in nests of stingless bees is this system in reverse. The cells open upwards and the stories are placed one above the other, the ground story being the foundation story. That, at least, is the almost unanimous interpretation of those who had opportunity to observe nests that were in process of construction. It is true that a few have formed a different conclusion. Thus Gronen (1881c, p. 111) cites Goudot to the effect that the lower combs in a nest containing 12 combs seemed to be those last constructed. It is also to be noted that in

their representations of hives the ancient Maya showed the combs attached to the ceiling and depending downward although, amazingly enough, they likewise showed a comb attached to a wall of the hive (Tozzer and Allen, 1910, pl. 2, figs. 7, 10). On the other hand, such observers as F. Smith, Hannemann, H. Müller, Drory, Tomaschek, Hockings, Peckolt, Williams, and Rau bear testimony to the fact that it is the upper combs that are deferred to the last.

Thus F. Smith more than 80 years ago (1863c, p. 174) demonstrated this method of building in the case of a nest of the Old World *Trigona carbonaria* F. Smith exhibited before the Entomological Society of London. "On the upper (or free) side," noted Smith, "was a quantity of matter of a coralline structure, which was apparently made for the purpose of carrying the nest up to the top of the box, and thereby of attaining additional support." Later (1863d, pp. 181-182) he was even more emphatic, asserting that "the combs are built over each other, the lower comb being first constructed so that it [the nest] increases in size upwards."

Regarding the same species, *carbonaria*, Hockings (1884, p. 150) confirmed the observation of F. Smith, stating that the building "commenced from the bottom and conducted upwards," but he extended this observation to include also nests of the Australian "kootchar" (*Trigona cassiae* Cockerell), a species that, as already indicated, builds its brood cells not in tiers but in clusters. Hannemann (1872, p. 207) indicated this was the procedure, too, in nests of New World *Trigona*.

Evidencing the fact that the erection of the successive stories of the nest begins at the bottom is the statement of Peckolt (1894, p. 224) regarding a colony of *Trigona (Trigona) ruficrus* (Latreille) which, like the *carbonaria* nest exhibited by F. Smith, was located in a box. In a little more than two weeks from the time the box was occupied by the colony, the nest rose to a height of 20 cm. At that stage the involucre did not completely envelop the brood chamber, which was "still open above, with the result that one was able to see the cell arrangement."

The speed with which the construction of brood combs takes place has been recorded also by Tomaschek (1880, p. 60) in the case

of what he designated *Trigona (Paratrigona) lineata* (Lepeletier) but which was almost certainly a different species, possibly *Trigona (Paratrigona) opaca* Cockerell. To complete the 19 stories of its nest this colony required 122 days, or an average of 6.5 days per comb. The rate of construction was, however, not uniform. In the beginning two combs were constructed in three days; later four days were devoted to the building of a comb. From September 5 to October 4 a total of five combs were built, among which were the largest of the combs. The last five combs required 57 days for their completion. Thus the workmanship was most rapid in the start but fell off as the edifice increased in size. Tomaschek was under the impression that high temperature was conducive to more speedy accomplishment.

Tomaschek's account clearly indicates that the building proceeds from below upward. By November 30 the nineteenth and final comb to be built "almost attained the lid of the box." Williams, too, contributed (1928a, p. 173, pl. 31 on p. 160) convincing evidence to the effect that stingless bees build upward, not downward, in erecting the successive combs of the brood chamber. He came upon a nest of *Trigona (Tetragona) jaty* F. Smith in which the topmost comb was only just begun. It consisted merely of four cells, three of which had not yet been closed, and it was obviously of very recent construction. Rau (1933, p. 23) indicated that comb was placed upon comb in close juxtaposition in a nest of a member of the subgenus *Partamona* he examined while in the Canal Zone.

Both Drory (1877, p. 115) and H. Müller (1875b, p. 46), who were among the earliest to affirm that the structure of stingless bees rises from below instead of descending from above, made notation of some details of the workmanship. Thus Drory stated that, while brood in one comb is maturing, other combs are constructed above. H. Müller, on the other hand, is even more specific, affirming that the second story is started as soon as the first story has attained a certain size, the foundations of the second story being laid at the middle of the first. Thereupon, while the second is still in process of construction and before the first has been completed, the third story may be started in its turn at the middle

of the second one, with the result that it is possible to have three stories all in course of erection at the same time.

The manner in which the stingless bees prepare the cells of each comb is told by H. Müller (1875b, pp. 45-46): "They begin the construction of each of their horizontal brood combs with a single cylindrical cell, which constitutes the middle of the future brood comb. After this cell has been provided with larval food and an egg and has been sealed, there is built close to it a second cylindrical cell, which flattens itself only along the surface of contact with the first cell. After this second cell has also been provisioned and closed, there are constructed simultaneously, in the two emarginations between the first two cells, two new cylindrical cells, which in their turn are flattened along the surfaces of contact with the already existing cells. After the provisioning and closing of these cells a new cell is placed in each of the now available four emarginations and this group of four cells in turn is wholly completed, provisioned and closed before the following cell group, which has to occupy the six emarginations now available, is undertaken; and so on. Each cell is thus cylindrical except in so far as its sides have not been flattened by pressure against neighboring cells; but each cell becomes irregularly hexagonal as soon as it is surrounded by six neighboring cells. . . . The outermost cells are in consequence always rounded cylindrically even when the entire comb has been completed." Incidentally Darwin (1859, pp. 225-226) indicated that likewise in the case of the provision pots, which he terms "cells," the contiguous surfaces tend to be flat. Thus "each cell consists of an outer spherical portion and of two, three, or more perfectly flat surfaces, according as the cell adjoins two, three or more other cells." But Darwin implied that these flat surfaces were thus built by the bees themselves instead of being due to lateral pressure.

From H. Müller's account as above cited, it is clear that not only the construction of the brood cells but also their provisioning proceeds from the center towards the periphery of the comb. Hence the slightly more mature brood tends to be near the center, the less-developed brood towards the outer extremity of the comb. In addition to this

gradation of maturity within a given comb, there is likewise a gradation of maturity from one comb level to the next comb level; the lower combs, being of earlier construction, are also those that have a head start in bringing to maturity the brood which they house.

While it is the usual method in the case of *Melipona* and of many *Trigona* to build from the center outward, new cells being constantly added to the expanding periphery, H. von Ihering (1903, pp. 251-252) was of the opinion that certain *Trigona*, at least, proceed along a different plan. In these cases the prospective comb first presents itself as a strong membrane of wax, which he designated the trochoblast. On this trochoblast, according to von Ihering, are indicated by means of delicate lines the boundaries of the future cells. The construction of the cells, he contended, is effected in the following manner: that part of the wax membrane that covers the space to be occupied by the future cell is removed and fashioned into a hexagonal belt, which in the initial stages rises only a little above the trochoblast but gradually is enlarged above and below until it takes shape as a completed cell. As a rule one such cell after another is set up in regular order but it sometimes happens, according to von Ihering, that at some distance from the main group of cells a single cell may be started. As the boundaries of the cells are marked out in advance, such an irregularity cannot, however, cause a disarrangement in the symmetry of construction. The existence of a trochoblast he verified in the case of what were identified as *Trigona jaty*, *cupira*, *dorsalis* (*postica*?), and *molestia*. Yet, while the trochoblast is, it is intimated, usually constructed anew, it is sometimes retained from a previous brood period, being merely cleared of the larval skins of the first occupants and reinforced by a coating of wax.

Somewhat mystified by the hexagonal tracings noted by von Ihering on the trochoblast, Bischoff (1927, p. 290) suggested as one of two alternative explanations the possibility that these tracings were due to the imperfect removal of the previous trochoblast, on which the original cell pattern is consequently still discernible notwithstanding additions of fresh wax. Supporting this in-

terpretation is the following observation of von Buttel-Reepen (1915, p. 232) on a nest of *Trigona*: "I found in a nest the horizontal floor level of a comb overlaid with a fine hexagonal network of lines that looked deceptively as though it were the ground plan of a new construction of cells, in other words the design of the future cells. If that had really been the case, the bees would in fact have the capacity to set down the angles with extraordinary skill and in a 'free-handed' manner and for the whole comb at once, but a closer inspection showed me that it was a question merely of almost completely removed old cells that had attained their hexagonal shape through counter pressure and whose surviving cell boundaries still remained on the floor of the comb."

After the brood has emerged, the cells that contained the brood are not utilized a second time. Indeed removal of the walls of the cell begins even before the maturing bee has crawled out. According to F. Poey (1852, p. 164), speaking of *Melipona beecheii* variety *fulvipes* Guérin, the removal of the waxen cap of the cell is undertaken progressively as the larva gains in age, so that when the larva has attained the nymphal stage, the cap has disappeared in its entirety. Poey confirmed the impression that the cells near the center of the comb are the first to be vacated and destroyed, and indicated that from this denudation of the central area the erroneous conclusion may be drawn by some that the activities proceed from the circumference to the center instead of vice versa.

Very possibly an observation of F. Müller (1874b, p. 103) based on a *Trigona* which he referred to as "mirim" [probably *Trigona* (*Plebeia*) *minima* Gribodo] is tinged with the misunderstanding to which Poey alluded. "There is always," wrote Müller, "in this species (other species behave differently) a set of cells constructed at the same time in the circumference of the two to three uppermost combs."

Although F. Poey indicated that the wax of the brood cell is removed progressively as the insect enclosed by the cell gains in stature, most observers have indicated that the process of demolition is deferred until the larva has spun its cocoon, and this would seem to be the more plausible procedure. F.

Müller (1875, p. 296) stated that the gnawing away of the wax cells is achieved at that time, and there then remains of the cell both above and below only the paper-like fabric of the larva. Hockings (1884, p. 153) stated of the Australian "kootchar" (*Trigona cassiae* Cockerell) that, "when the young have reached the second stage of their existence [by which almost certainly he means the pupal stage] the wax is almost wholly removed from the cocoon." Friese (1914a, p. 44) cited Jacobson to the effect that *Trigona* (*Tetragona*) *iridipennis* F. Smith removed the outer wax from the cells as soon as the cocoon is spun by the larva occupying the cell. Traces of wax nevertheless remain, according to Friese, on the cocoons, which are of a yellowish white color. According to the observations of Rau (1933, p. 23), on the other hand, the adult bees do an efficient job of removal, "the lower comb is composed entirely of rows and rows of pupal cases, and not a vestige of wax is to be seen." Rau's observation was made on a member of the subgenus *Partamona* in the Canal Zone, whereas Friese's statement applies to the Old World *Trigona* (*Tetragona*) *iridipennis* F. Smith. Perhaps the more superficial removal of the wax in the case of *iridipennis* is linked with the fact that this bee builds cells that are not arranged in combs but irregularly in clusters, where the support of the wax is still required for the maintenance of the constituent cells as a group. At any rate, even though much of the wax is removed in the case of a nest of the cluster type, the thin wax pillars are apparently retained as essential structural elements. This, at any rate, was the condition in the nest of *iridipennis*.

Note has been made above of the practice of *Melipona beecheii* variety *fulvipes* Guérin in removing wax progressively from the cell as observed by F. Poey. In the case of the closely related *Melipona interrupta* variety *sali* Schwarz, Salt (1929, p. 436) noted that "In the older tiers where the larvae were full-grown and had formed their cocoons, the cerumen had been removed from the tops and bottoms of the cells and the edges of the tiers, leaving the light brown cocoons exposed and free of wax on their outer surfaces." Salt thought this removal might have been exceptional owing to special circumstances, but

the fact that the same phenomenon has been observed again and again in a diversity of stingless bees makes such a conclusion unlikely. More probably the practice is fairly general throughout the family.

Even the floor of the cell often is finally removed, and this may take place while the part of the comb adjacent to the circumference still contains brood. In such cases a ring-shaped rim may surround a demolished, more or less disk-shaped central area. Several such ring-shaped combs are sometimes found in the same nest, one above the other but of varying breadth (H. von Ihering, 1903, p. 250).

There can be little doubt, in view of the number of observations made, that the waxen cell is removed more or less completely after the larva has spun its cocoon. But what happens to the cocoon itself after the emergence of the adult insect? According to Hockings (1884, p. 155), who recounted the habits of the "karbi" (interpreted as *Trigona carbonaria* F. Smith) and the "kootchar" (*Trigona cassiae* Cockerell) the vacated cocoons "are removed and placed in a heap, each being rolled into a ball; this heap is reduced by fits and starts, and is sometimes not touched for as much as a month."

THE AGE OF NESTS AND SOME SPECULATIONS REGARDING THE ROYAL CASTE

Not only are *Trigona* nests sometimes very large from the standpoint both of the number of stories or combs and of the population housed; they may also have had a continuous history over a considerable stretch of time. Certain of the nests on Barro Colorado Island, Canal Zone, have occupied the same site year after year. I am thinking particularly of the nest of *Trigona* (*Trigona*) *fulviventris* variety *fulviventris* Guérin in the "Allee tree"¹ and of a nest of *Lestrimelitta limão* (F. Smith) near "6"² on the Allison Armour Trail, which were just as thriving seemingly on my second visit to Barro Colorado Island as they were on my first

sojourn there three years prior. Nests of *Trigona* (*Trigona*) *corvina* Cockerell have been reported, one of them in the Canal Zone allegedly at least six years old (Rau, 1933, p. 36), the other noted in a letter received from Nevermann in Costa Rica as "a ten-year old nest." A nest "known to be at least 10 years old" is reported in a letter by C. D. Michener. Surrounding a grapefruit branch in a grapefruit orchard at Juan Mina in the Canal Zone, this stupendous nest weighed 69 pounds.

Somewhat disconcerting, it must be confessed, to the theory that nest populations are continuous over long stretches of years are the searching field studies of Michener in Panama (1946, pp. 182-183). In a section of his paper headed "Longevity of colonies" he offers incontrovertible proof that what we mistakenly believe are colonies with an unbroken history may be instead, in some instances at least, successive occupations of the same nest by newcomer swarms of the identical species, each swarm taking possession in its turn of a homestead devoid of living occupants. Yet a person who examined the nest only at the beginning of its history and again towards the end would be under the illusion that one colony, not several in succession, had been in continuous possession of the nest. In one instance, Michener related, a nest of *Trigona* (*Tetragona*) *jaty* F. Smith was occupied by three different colonies of that species during a period of 14 months. Residence was not continuous, however, there being intervals of months during which the nest was tenantless. Similarly a nest of *Trigona* (*Nannotrigona*) *testaceicornis* variety *perilampoides* Cresson after being "to let" from at least September 28, 1945, to some time prior to December 31, 1945, was taken over by another colony of the same species and variety. Notwithstanding these evidences of an interrupted history of nest occupation, one may still wonder whether they are not the exception rather than the rule and whether in other instances, when a nest of long duration has been noted, such a nest is not one that has been in continuous possession of the original settlers and their descendants rather than of successive independent swarms.

The records of the old age of hives in the wild state are overtopped by the reports of

¹ A habitat group illustrating the external appearance of this nest has been installed in the American Museum of Natural History.

² The trails on Barro Colorado are marked at regular intervals by numbers.

enduring communities in the case of domesticated nests. A domesticated hive of *Melipona fasciata* variety *guerreroensis* Schwarz, I am informed by A. Dampf, had been maintained by an Indian family at Taxco, State of Guerrero, Mexico, for more than 10 years. J. Pierre Huber, who was the recipient through a Mr. Forbes of information supplied by beekeepers of Tempico, Mexico, referred (1839, p. 22) to the artificial hives of *Melipona beecheii* Bennett as "perpetual." There was one hive of this species to which an age was attributed of more than a century. One may express doubt as to the accuracy of this record and yet remain convinced that it must have been a very old hive.

Even if we discard the centenarian and confine ourselves to hives no more, allegedly, than 10 years old, an interesting problem presents itself. In the honeybee it is the old queen that leads the swarm from the parent hive in quest of new quarters, while her place in the vacated old homestead is taken over by one of her royal daughters about to emerge from her cell. Although Peckolt (cited by F. Smith, 1868, pp. 133-134) tended to convey the impression that among stingless bees swarming took place under the leadership of the old matriarch, other authors (Drory, 1877, p. 146; Silvestri, 1902b, p. 166; von Buttel-Reepen, 1903a, p. 141; H. von Ihering, 1903, p. 181; Handlirsch, 1926, p. 112; Bouvier, 1926, p. 159; Wheeler, 1928, p. 101) have indicated that, reversing the condition in *Apis*, it is the young princess that goes forth with the attendant swarm in quest of a new home. Indeed, it is hard to believe that the gravid queen is capable of flight, so short and inadequate do her wings appear when contrasted with the swollen and distended abdomen. Often the wings, in addition to being short, are frayed or reduced to impotent vestiges of the original flight organ and would seem utterly useless for sustaining the weight of the egg-laden insect.

If the old queen, however, is committed, as H. von Ihering puts it, "to life-long confinement" within the nest (1903, p. 181), is she destined never to be replaced in her activities? Is the life of the nest coterminous with that of its royal founder? If there be nests that are indeed 10 years old or older, is the fecundity of the queen maintained through all this long

stretch of time notwithstanding the drain of egg laying to maintain populations that sometimes run into the tens of thousands? The queen of the honeybee may live from three to five years. Is the queen of the stingless bee granted a life and a capacity two or three times that of the corresponding caste of the genus *Apis*?

The general impression is that among the stingless bees there is only a single gravid queen to a nest, an impression based on the study of many colonies (Klug, 1843, pp. 219-221; F. Poey, 1852, p. 154; F. Smith, 1866, pp. 325-326, and 1868, pp. 133-134; Drory, in Raveret-Wattel, 1872d, p. 683; H. Müller, 1875b, p. 43; F. Müller, 1875, p. 296; Holmberg, 1887, p. 255; Peckolt, 1894, p. 88; Silvestri, 1902b, p. 166; von Buttel-Reepen, 1903a, p. 135; Marianno, 1911, p. 45; L. Martin, 1930, p. 98). Against this formidable array of opinion there is some dissent. Even F. Smith, whose name has just been cited in support of the view that there is but one physogastric queen to a nest, was originally (1863d, p. 182) "inclined to the opinion that the hive of *Trigona* contains several prolific females; the accounts given of the multitudes inhabiting some nests is too great, I think, to render it possible that one female could produce them all." This statement of Smith was, however, based not on observation but on assumption and so carries little weight against his later and more mature conclusion based on actual examination of conditions. Schulz (1905c, p. 140), on the other hand, wondered whether to interpret as virgins or as physogastric queens three members of the royal caste in a colony of *Trigona* (*Partamona*) *testacea* variety *cupira* F. Smith. Schulz dwelt on the inflated condition of the abdomen of these three individuals and left the reader under the impression that he inclined to the view that the queens were gravid. The photograph Schulz reproduced (1905c, fig. 13) does not, to me, suggest a physogastric queen. More confidently positive is Castets (1893, p. 485; 1908, p. 53), who asserted of *Trigona iridipennis* F. Smith that "The simultaneous presence of several fertile queens is a quite ordinary occurrence with this *Trigona*," a conclusion that no other observer of this species has confirmed. The claim that there are multiple gravid queens in a colony is in

need of further substantiation before it can be accepted unchallenged. Certainly the usual condition is a single gravid queen to a nest.

It is well verified, however, that, in addition to this single physogastric queen, there are frequently found in the nest of stingless bees a rather impressive number of royal daughters, living seemingly in amity with their mother and their sisters in contrast to the condition in the honeybee colony where the queen is intolerant of a royal rival and the first princess to emerge, after the departure of the queen mother with her swarm, frequently commits regicide, soricide, and adolescenticide combined, by stinging to death her sisters of the royal brood often even before these have had a chance to emerge from their cells. May it not be, therefore, that in the event of exhaustion or death of the mother, her functions are taken over, in the case of the more tolerant stingless bees, by one of the younger members of the royal line? (See also p. 157.)

If such substitutions do not occur and the spirit of amity is maintained within the royal circle, one is a little puzzled regarding the ultimate destiny of the princesses. Even granted that such substitutions may occur, the number of these individuals sometimes seems out of proportion to the requirements both of successive swarming and of possible substitution within the old nest. Thus Drory counted 30 maiden queens in a colony of *Melipona* (von Buttel-Reepen, 1903b, p. 52). In a nest of *Melipona interrupta* variety *salti* Schwarz that Salt observed (1929, p. 435) 15 young queens were noticed, and among the 25 adults that emerged the fourth day after the nest was taken five were queens. Twenty-six royal cells were noted by the same observer (1929, p. 439) in a nest of *Trigona* (*Trigona*) *amalihea* (Olivier). It was estimated by H. von Ihering (1903, p. 230) that there were possibly two dozen royal cells in a nest of *Trigona* (*Trigona*) *ruficrus* (Latreille), and a somewhat similar total was arrived at by Silvestri (1902b, p. 137) in studying a nest of this species. In a letter I received from Mr. R. G. Donald mention is made of a nest of *Melipona favosa* variety *favosa* (Fabricius) observed on Trinidad Island which had 28 virgin queens. The most astonishing repre-

sentation of young queens is reported, however, by F. Poey (1852, p. 153), who, in a nest population of *Melipona beecheii* variety *fulvipes* Guérin that included 600 to 1000 workers, claimed that he found no fewer than 40 virgin females, at first misinterpreted as males (F. Müller, 1875, p. 293). Even this total was, however, exceeded in another nest reported by F. Poey (1852, p. 158) in which there were allegedly 50 virgin queens, although the total population of the nest was much greater than that of the first nest mentioned, possibly as much as 4000. If these figures are accurate, they leave one puzzled by the prodigality of nature in connection with a caste for which there is only limited requirement. It is possible, however, that, in addition to their preëminent function of ultimately founding a nest of their own, these unmated royal daughters, during their sojourn in the maternal nest, may lay eggs that develop into drones. This, at least, was the surmise of Drory, who was inclined to speculate that their role might be dominant in this respect (Drory, 1872b, p. 188; Raveret-Wattel, 1872d, p. 688; Drory, 1874, p. 286). F. Müller, too, toyed with the possibility (1878, p. 230) that in these aggregates of unmated females we might have a group dedicated to the sole object of laying unfertilized eggs that would develop into drones. He even coined for them the rather grandiloquent title of "holy maidens," hoping thereby to escape the polysyllabic and breath-consuming "parthenogenetic females" more generally in use. But on the whole he was more inclined to the belief that these individuals were merely unmated queens and not permanent celibates.

A curious observation regarding the virgin queens is contributed by Drory (1874, p. 286). Although the royal mother seemingly tolerates the princesses, the commoners of the state occasionally maltreat them. "Often have I observed," stated that author, "in the case of my own colonies that the workers pursued the virgin queens, or drove them away, or even killed them. Whether the local temperature conditions were a contributing factor, or whether it is their habit to behave thus also in Brazil, my friend [Brunet] will inform me at some future time."

HAPPENINGS OF THE COLONY

MATING

It is natural to begin an account of the life of the colony with its inception but, like many beginnings, the act of mating, which is fundamental to the existence of the colony, is veiled in obscurity. We do not know whether it takes place on the wing, as is the case in the honeybee, or on the leaf or branch of a tree after the manner of some bumblebees. It is even possible that it is consummated within the shelter of the nest itself. However, more probably it occurs in the open, for virgin stingless bees have been observed away from their home surroundings and without accompaniment of workers, and such independent venturing forth suggests a mating quest.

According to J. M. Pérez (1895a, pp. 273-275; 1895c, pp. 125-126) a virgin queen of "a little *Trigona* from Uruguay," the only virgin queen observed in the hive during 1893, disappeared from the nest at the end of September, "having gone out during bright sunshine to take, according to the expression customary in apiculture, her nuptial flight." Pérez went on to say that this royal member did not return to the hive, and his assumption of a nuptial flight was seemingly inferential and not based on actual observation.

Another member of the royal caste (in this case *Melipona mondury* F. Smith, which is considered very close to *fasciata* variety *rufiventris* Lepeletier) was collected by F. Müller (1878, p. 229) "in the open." I think it may be assumed that the bee was taken independently of a swarm, otherwise certainly that circumstance would have been mentioned.

Recently I have received from Mr. R. G. Donald a queen of *Melipona favosa* var. *favosa* (Fabricius) caught at Manzanilla, Trinidad, British West Indies, on February 4, 1945. It, too, was unaccompanied by workers, and one is tempted to think that it went forth to mate, as the queen is obviously incapable of foraging and would have no other functional urge for leaving the hive except mating.

Mr. Donald, to whom I wrote in the hope of obtaining further details regarding his interesting catch, has supplied the following state-

ment: "On 4th February 1945, at about 6:30 P.M. when it was already beginning to grow dark, I noticed the insect, which I could not see sufficiently well in the bad light to be sure whether or not it was a bee, flying slowly around at a height of about 2-3 inches above the loose gravel of the road, a few yards from the edge of the beach [Manzanilla is on the east coast of Trinidad]. I was surprised that it *was* a bee moving at that hour and could see nothing by which it might have been attracted to the spot, e.g. picnic scraps with jam."

Fecundation of the virgin queens takes place, according to Bouvier (1921, p. 211), in the spring or summer, when the males make their appearance, but he does not indicate where this act is achieved and presumably based his statement on the simultaneous presence of the two sexes at that time of the year.

At first thought it seems inexplicable that among the many species of stingless bees that inhabit the tropics there has seemingly never been observed an act of mating. Yet the failure to note this happening loses some of its strangeness when we reflect on the centuries that went by before man learned of this occurrence in the case of the honeybee, an insect domesticated by him since time immemorial. So completely was the mating act withheld from human eyes that the great Swammerdam, who studied the bees with unremitting devotion, nevertheless entertained the notion that the queen was impregnated by an odor emanating from the drones rather than by an act of copulation, and the English naturalist DeBraw, similarly baffled by the failure of anyone to witness a mating, concluded that the male fertilized the egg after the manner of frogs and fishes by bedewing it with a sort of milt-like secretion. Through the ages, too, there persisted the incredible belief that bees were generated within the carcass of an ox. In "pooh-poohing" this notion Florinus, at the beginning of the eighteenth century, thus accounted for the prevailing ignorance regarding the mating of the honey bee: "On account of the modesty of the creatures, the copulation has never been seen"

(cited by Ransome, p. 154). It was not until nearly the end of the eighteenth century that the inquiring and inventive mind of François Huber with the indispensable aid of his painstaking partner, Francis Burnens, at length devised a series of ingenious experiments that definitely proved the conjectures of others to be false and gave ocular proof of the true happening. Perhaps a Huber is needed to probe the mysteries, too, in the love life of the stingless bees.

CASTE PRODUCTION AND NUTRITION

In the honeybee all castes (worker, queen, and drone) receive the same diet initially, namely, a salivary secretion of the adult worker bee that is known as "royal jelly." From the fourth day onward (the third day onward according to Lineburg) the drone larva and the larva that is to develop into a worker receive a change of diet, while the larva that is to be reared as a queen continues to receive royal jelly, although a few undigested pollen grains may find place in that regal food (Phillips, 1928, pp. 123-124). The somatic differences between the worker and the queen seem to be traceable to this difference of diet, for an egg or a young larva that is transferred from a worker cell to a queen cell develops not into a worker but into a queen. Thus the factors that govern the emergence of a queen or of a worker seem in the case of the honeybee to be nutritional, and not due to any difference in the egg.

It is otherwise with the stingless bees. In their case there is mass feeding, not progressive feeding as in the honeybee. The general belief is that the supply of pollen and honey that will serve the larva during its prepupal life is all put in the cell in advance. It is only when the larder is thus stocked that the egg is laid, whereupon the top of the cell is usually sealed over and all contact with the outer world is shut off until the larva, having attained adult status, emerges from the cell a winged insect.

In the genus *Melipona* there are no royal cells; the cell that houses a future queen is identical in appearance and not to be differentiated from the cells that confine the commoners of the bee state. The food with which the cell that is to contain the royal caste is stocked does not differ quantitatively and is

generally not believed to differ qualitatively from that placed in similar cells from which eventually will emerge an adult worker or a male. Hence the environmental conditions and the food being the same in each case, the emergence of a queen or of a worker must be due, it is claimed, to factors other than nutritional in the genus *Melipona*.

In the genus *Trigona* there are royal cells that exceed in size those of the other two castes, but the cells of the workers and males at least cannot be differentiated from each other. The larger size of the royal cells is correlated with the fact that the queens of *Trigona* tend to be larger than the other members of the colony and so require more space to accommodate their greater bulk. But, again, the food given the larval queens of *Trigona* is generally thought to be qualitatively the same as that amassed for the larval workers or for the larval males. As a result, the temptation is to conclude that the differences of structure that are noticeable as between queen and worker are, as in *Melipona*, probably predetermined in the egg.

J. M. Pérez (1895a, pp. 273-275; 1895c, pp. 125-127) watched for possible happenings in a queenless colony of a small *Trigona*. Workers of *Apis* under similar conditions would strive to rear a new queen through continuous feeding with royal jelly. But the *Trigona* workers were apparently impotent to achieve this result, and Pérez stated confidently that "*Trigona* is incapable of replacing the vanished mother of the nest." Pérez' observation might seem to give support to those who believe that the diet for all the castes is uniform in the Meliponidae, for, were a special secretion responsible for the development of the royal caste, surely it would be employed, as in the case of the honeybee, to assure the perpetuation of a queenless colony through the rearing by special feeding of a royal successor. But the case of the honeybee and that of the stingless bee are not wholly comparable. In the honeybee the cell containing the larva is open, the feeding of the larva is progressive and can therefore be adjusted to produce a member of the royal caste. In the case of the stingless bees the cell is stocked with food, supplied with an egg and sealed, thus barring a later change of diet.

Daughter colonies of stingless bees have

been started by removing from the parent hive some of the brood combs and provision jars and a nucleus of adult bees. Such daughter colonies have thrived, notwithstanding the fact that they were initially queenless. They have given rise to queens in course of time even though only workers presided over the nest. Workers throughout the social Apoidea, so far as known, lay eggs that yield males only. Hence concluded some entomologists (Figuier, 1872, p. 357; Girard, 1866, p. 168; 1879, p. 721) it must be that under stress of necessity the stingless bees know how to produce a queen, "probably by a special paste." The fallacy of this conclusion, it would seem, is that in such a colony as that described, started through the transfer of combs to a new nest hollow, there is presumably neither feeding nor laying of eggs until a queen emerges, and so the emergence of a queen traces back to events prior to the parturition of the old nest, and is not affected by events taking place in the new nest.

But are we certain that progressive feeding does not take place, to some extent at least? A dissenting view as to the uniform character of the food given to all castes and as to the immediate closing of the brood cells when they are stocked is expressed by Rayment (1932b, pp. 9-10; 1935, pp. 539-540).

"It has been contended over and over again by authors," stated Rayment, "that the larvae of *Trigona* are supplied solely with honey and pollen; the cell being sealed immediately. My observations of *T. cassiae* and *T. carbonaria* show that while the brood-cell is half-full of food before the egg is deposited—which is in sharp contrast to the practice of the hive-bee—the cells are not sealed at once, and I have many times recorded larvae, up to three days old, feeding in open cradles. Some 'afterfeeding' does take place, and the food furnished to the larvae is not exclusively honey and pollen, but has some other biological substance added to it by the worker-bees."

Rayment (1935, p. 542) characterized this "biological substance" as potent but "not so 'rich' as the 'pap' of the beehive."

Rayment's observations are a stimulus to further investigation. If, indeed, there is some secretion or product that supplements

the diet of honey and pollen, it may be that to it are traceable, as in the case of the royal jelly of the honeybee, the differences that obtain between queen and worker. Bouvier (1926, p. 38) also hazarded the surmise that before the egg is laid each cell receives, in addition to the lump of pollen and honey, some fluid nutriment, "proceeding doubtless from the salivary glands" of the workers. Several writers, beginning with Drory, have indicated that the more fluid part of the food content of the cells constitutes the upper layer of nutrition, and if, indeed, it should prove that a glandular secretion enters into its composition, then the emerging larva, in contact with this upper layer, would presumably, like the honeybee larva, first consume this special diet before being weaned to honey and pollen.

Of possible bearing, too, upon this interesting subject are the comments of H. von Ihering (1903, p. 269): "I have noticed on several occasions that new brood combs in the first stages of their development, when they are easily injured by bending, emit at the injured spot a clear liquid, which is nothing else but the juice with which the pollen mass is mixed to obtain the food pap of the larvae. This fluid has a very sour taste and leaves behind, when it evaporates, a white, sour-tasting powder, which, according to Peckolt's investigation, is a formic acid salt." Here something other than honey, or at least additional to honey, seems to be involved.

The possibility that the production of castes in the Meliponidae may be owing to the food supplied rather than to differences in the egg is brought to the fore by comments just cited. However, Rayment's observations on the belated closing of the cells is at variance with the report of Drory, based on a study of *Melipona fasciata* variety *scutellaris* Latreille. According to Drory (1872b, pp. 203-204; 1873d, pp. 106-109; and cited by Raveret Wattel, 1872d, pp. 685-687), the following procedure occurs: As the workers complete a cell, the queen mother lowers her head and thorax into it by way of making an inspection. Thereupon five or six workers that did not participate in the construction of the cell come forth, and each in turn, after confronting the queen and being touched by

her antennae, thrusts her head into the cell and deposits pollen and honey. The cell is thus filled for three-fifths of its depth "with a solid material consisting principally of pollen and of a layer of limpid liquid of which the main constituent is certainly honey." The depositions of food are made in rapid succession, sometimes interrupted by inspections conducted by the queen herself, the whole procedure lasting about three or four minutes. The queen then makes a minute inspection of the cell, after which she introduces her abdomen into the cell and engages in oviposition for an interval of about 30 seconds. Then she raises herself, takes a look at the egg she has laid, and proceeds to the next cell to make the same inspection and effect another laying.

As soon as the egg is deposited and the queen has left the cell, a worker that has been awaiting this moment mounts the cell and begins the work of sealing it. She places her abdomen in the orifice of the cell and proceeds to make a complete turn about herself while biting at the edges of the cell, which are bent lightly inward. As she works, the border of the cell becomes more and more flattened. With her abdomen, the extremity of which is still in the cell, she seems to apply the counter pressure to that which she exercises with her mandibles in fashioning the cover. The orifice grows ever smaller and her abdomen is progressively withdrawn, at length wholly so. There then remains only the task of closing the narrowed hole, which the worker does with the aid of her mandibles and fore legs. All of this is achieved, stated Drory, in less than the interval of time that the mother takes to lay an egg.

Essentially the same account as that given by Drory is contributed also by Girard (1875a, pp. 569-570). Hockings (1884, p. 153) in general confirms this picture as to the procedure in closing the cells in the case of the Australian species of *Trigona* known as "kootchar" (*Trigona cassiae* Cockerell). If the worker engaged in closing the cell is forcibly removed, she is immediately replaced by one of her fellows. But never is there, according to Hockings, more than one bee participating in the sealing of a cell. It would seem, however, that not always is the task the exclusive prerogative of a single bee, for Brunet, as cited by Drory (1873a, pp.

xxx-xxxii) noted that the bee entrusted with the closing of the cell is aided initially in the operation by one of her companions. This was observed by Brunet in the case of a *Trigona* known in Bahia, Brazil, as "tiuba amarella," probably *postica* Latreille or close to it.

The description that F. Poey (1852, p. 164) gave of *Melipona beecheii* variety *fulvipes* Guérin confirms the impression conveyed by Drory that each cell is supplied with food and egg as soon as it is completed. This is the procedure indicated also by H. von Ihering (1903, p. 251). On the other hand, F. Müller (1875, p. 297) was under the impression that such individual provisioning of the cells was the rule only in *Melipona*, while *Trigona* completed a number of cells before filling them in rapid succession. This contention receives some support from the observations of Williams (1928a, p. 173, pl. 31), who described and figured a nest of *Trigona* (*Tetragona*) *jaty* F. Smith, in which three of the four cells that constituted the uncompleted topmost comb of the nest were still open at the time the nest was examined.

Those who believe that the food is uniform in character and that the caste differences reside in the egg are doubtless governed somewhat by the fact that, in the method of feeding the larva by supply in mass instead of progressively, the Meliponidae are merely continuing the tradition of the solitary bees with no evidence of a break from that tradition. On the other hand, the fact that in both the honeybee and in the stingless bees the queen is structurally so different from the worker and shows to a large extent the same type of degeneration gives those a talking point who recommend caution in accepting as a finality the belief that the differences between the stingless bee worker and the queen spring entirely from differences inherent in the egg.

According to the observations of F. Müller (1878, p. 231) there is this further parallel in the life history of *Apis* and of *Melipona*: in both, the queen has the shortest pre-adult stage, the male the longest, while that of the worker is intermediate. Müller was inclined to believe that this identity of occurrence gave support to the interpretation that similar influences governed the development

of the castes in both *Apis* and *Melipona*. In the same article (1878, p. 231) F. Müller even attempted to account for the fact that the males and workers in some species resemble each other more than the queen resembles either by assuming that drones and workers received one type of food in the larval stage while the queen was given different nourishment during her early period of development.

The deposition of the egg seems to vary somewhat from species to species. Usually it is placed upon the mass of food accumulated in the cell, or, as Hockings (1884, p. 153) described the act of egg laying in the case of the "kootchar": "The egg is forced into the food by the queen, with one end slightly protruding." Its perpendicular position is mentioned by George (1934, p. 5) in the case of *Trigona* (*Tetragona*) *iridipennis* F. Smith. Salt (1929, p. 439) found the egg of *Trigona* (*Trigona*) *amalthaea* (Olivier) floating on "a very fluid food" with which the cell was filled to a depth of about two-thirds. The egg evidently was sufficiently light to be buoyed by the fluid, for it was not in any way attached to the sides of the cell. However, in some instances, it is claimed, the queen, instead of placing the egg on the provisions, seems to attach it to the inside of the lid of the sealed cell. This method of attachment was recorded by Rau (1933, p. 22) in the case of what was identified by me as *Trigona* (*Partamona*) *testacea* variety *cupira* F. Smith, although the bee in question is to be considered rather a new variety of *testacea*. This observation is the more puzzling because, until the worker has closed the cell by uniting the upper edges of the walls of the cell, a "lid" can hardly be said to exist.

DIVISION OF LABOR

According to the observations of G. A. Rösch on the honeybee there is specialization of function in the hive according to the age of the bee. In other words, the adaptation to a given task does not accord with morphological differences, as is the case among the ants and the termites, but is associated with different stages of development in the individual bee. As set down by Imms (1931, pp. 51-52) on the basis of the "useful summary of Rösch's work" prepared by D. M. T. Morland, the life of the worker honeybee may be

divided into three periods, which are as follows:

"First Period. The newly hatched bees prepare cells for the reception of the future eggs and also help in maintaining the right temperature of the hive. After the second day, feeding of the older larvae with honey and pollen is taken over, and this goes on until the sixth day. From the sixth, until about the fifteenth day, the pharyngeal glands are functionally active and the bees consequently devote themselves to feeding the very young larvae. By the end of this time the pharyngeal glands tend to atrophy and brood-feeding ceases.

"Second Period. This is inaugurated with the first flight from the hive, the so-called orientation flight. During this period the bees receive and store nectar from foraging bees: they attend to the pollen brought in and act as general workers in the hive. Bees of this age have their wax glands in the active secretory phase and whatever comb-building that may be required is carried out at this time. Toward the close of this period, which lasts for about 10 days, the bees may take on the function of guarding the hive entrance.

"Third Period. In this period, which is from 20 to 30 days' duration, the workers are active only in the field and are engaged in foraging for water, pollen, nectar and propolis. They continue at this kind of work until they die."

That is the life of the honeybee and, if we add to it retrogressively the pupal, larval, and egg stage that precede these adult activities, the honeybee, like man, may be said to have approximately seven ages. Can the same thing or anything like this conclusion be asserted of the stingless bees? We know too little about the capacities according to age of the Meliponidae to speak with finality, and yet there are hints here and there that special functions assert themselves at given times. The impression conveyed by Dreyling (1905, pp. 317, 319) is that only the younger adult Meliponidae are capable of producing wax owing to the fact that in old individuals the wax glands degenerate. Here would seem to be a definite case where a function is of temporary nature, and hence the activities associated with that function are similarly limited. Do stingless bees in the wax-produc-

ing stage confine their services to the nest? The answer of H. von Ihering (1886, p. 184), at least in so far as *Trigona* (*Trigona*) *ruficrus* (Latreille) is concerned, is "yes." This species is a particularly aggressive one and attacks with violence. Yet neither among those bees that venture forth to the assault nor among those far afield foraging are ever found, according to the observations of von Ihering, any that are producing wax. To obtain the latter one must open the nest itself and search the brood chambers, where these wax producers will be found engaged in building operations. From this von Ihering concluded that there was what he designates "dimorphism" among the workers, a division into wax producers and pollen gatherers. Schulz (1905c, p. 141) indulged in similar speculations regarding the possibility that some of the nest inmates are permanently committed to indoor tasks while others devote themselves to ranging the fields. But the far more likely explanation is that this division of activity is not permanent but is associated with successive stages of development of the individual bee, and von Ihering even admitted the possibility of such a succession of functions while holding to his theory of dimorphism.

Are we justified, then, in saying that the earlier adult stages in the life of the bee are spent, as are the egg, larval, and pupal stages, in the nest and that only as life advances are the indoor routine tasks exchanged for the free ranging of the sunny world outside of the hive? Almost one is inclined to say so, but in the same breath one must also voice a qualified doubt. Young adult bees are lighter colored than other adult members of the hive. Indeed, not a few so-called new species have been erected because the describer had before him an isolated callow or two instead of adequate material showing the many gradations of coloration from the callow to the fully darkened adult. Yet callows have been taken in numbers outside of the nest. A "swarm" of the Indo-Malayan *Trigona* (*Tetragona*) *fusco-balteata* Cameron that I had the opportunity of identifying (1939c, pp. 107-110) included specimens of more or less pallid abdomen as well as fully colored individuals. *Trigona* (*Tetragona*) *nigra* variety *paupera* (Provancher) has also been taken in large

flight groups and these have included individuals of nearly every stage of coloration. Salt (1929, pp. 442-443), who with a few swings of the net secured upward of 400 individuals from such a winged assemblage, analyzed them as follows:

Abdomen white above, remainder of the body black	282 individuals
Abdomen white above except for dark apical fasciae of the segments.	27 individuals
Abdomen gray above with dark apical fasciae.	15 individuals
Entirely black	78 individuals

The bees, among which, as the above tabulation indicates, callows greatly predominated, were "flying rapidly within a limited space about six feet square, passing and repassing each other, wheeling, turning sharply at the side, and darting swiftly back." Salt interpreted this strange flight as "concerned with maturation of young workers, previous to their becoming full-fledged foragers of the colony."

Long ago Drory (1873c, p. 173) recognized bees of pale abdomen and fully colored bees in what may well have been a colony of *Trigona* (*Tetragona*) *nigra* variety *paupera* (Provancher), but he was misled into believing that they constituted two different castes and that the individuals of white abdomen were the true workers. The reason for his conclusion was that the pallid specimens flew out of the nest with greater frequency than the dark individuals and produced wax.

A flight of orientation is made by the honeybee worker at the beginning of the second period of her activity as an adult and up to that time her tasks are confined to the nest. It would seem that stingless bees engage in some activities outside the nest at an earlier stage than do honeybees.

In fact, in the case of *paupera* there is a lingering doubt in my mind whether the callows confine their activities outside of the hive to such communal flight exercises as those noted by Salt. Among specimens of *paupera* that I collected on Barro Colorado Island, Canal Zone, outside of the nest is one with ivory white abdomen, and therefore plainly a callow, that nevertheless has its legs heavily smeared with a sticky substance that is almost certainly building material.

Perhaps this building material was picked up in the hive itself, but it suggests the kind of foraging that is usually done out in the open.

L. E. Cheesman (1933, pp. 57-58), who had under observation an introduced hive of stingless bees for more than a year, stated that both young and old adult bees participated in repairing the flight tube of their nest. For the purpose they would bring up gum, "a drop at a time from the depths of the nest." She differentiated the new workers "by their brighter colour and entire wings (for the old workers had ragged edges to their wings)." It is not clear, however, whether by "brighter colour" the author intended to imply merely a fresher appearance or was emphasizing an actual difference in coloration suggestive of the callow. The fact that the wings were in certain individuals unmutated would not be proof positive, it seems to me, that the bees thus characterized had not used their organs of flight for ventures outside of the nest.

Tending to suggest, however, that foraging for pollen, at least, is rarely indulged in, if at all, by young adults is the record I took of pollen laden *Trigona* (*Tetragona*) *nigra* variety *paupera* (Provancher) returning to a nest on Barro Colorado Island, Canal Zone, from 9:30 A.M. to 11:30 A.M. on March 2, 1933. In all cases the bees carrying these burdens back to the community were fully colored specimens; there was not a callow among them. The number of laden foragers returning was fairly constant from half hour to half hour with a slight increase in numbers as the morning advanced. Thus between 9:30 A.M. and 10 A.M. I counted 22 pollen bearing bees; between 10 A.M. and 10:30 A.M., 23; between 10:30 A.M. and 11 A.M., 28; between 11 A.M. and 11:30 A.M., 30. After 11:30 A.M. activity fell off considerably. Between 11:30 A.M. and 12 noon only 15 laden bees returned. In the afternoon only six pollen bearing bees entered the nest between 1:45 P.M. and 2:15 P.M.; five between 2:15 P.M. and 2:45 P.M.; eight between 2:45 P.M. and 3:15 P.M. All were fully colored individuals.

The above record is, of course, far from conclusive, being based on only one species and involving observations too limited in time. It is in order to recall that among bumblebees, at least, there is an occasional

example of precocious activity in the field. Although two or three days are required for an emerged bumblebee to attain its full color, Plath (1934, p. 12) noted a worker belonging to an incipient colony of *Bombus separatus* Cresson which "was seen returning to the nest with a load of pollen when but two days old."

INTOLERANCE OF LIGHT

The urge to go forth into the world of flowers seems from a human point of view a natural one. We think of the bees as sun worshippers and, indeed, except for a night flying group like the members of the genera *Megalopta* and *Xerophasma*, and a few other forms that are crepuscular, they are creatures of the sunshine, conspicuous on fine days, disappearing with cloudiness or rain. And yet in a way this association with the sunshine is something of a mystery, for in the nest the bees are intolerant of it. In this respect the stingless bees differ little from the honeybee. They will seal up every crevice to keep out the rays and in an observation hive will cover the wire mesh that encloses their nest with a concealing sheet of wax or similarly dim out the window pane through which the observer hopes to make his observation. According to Rayment (1932a, p. 246; 1935, pp. 529-530) the most cautious uncovering of the glass shielding the side of an artificial nest or the removal of one of the detachable walls always created pandemonium. No amount of handling of the species involved (*Trigona carbonaria* F. Smith or *Trigona cassiae* Cockerell) made the bees more tolerant of light, whereas hive bees, although at first showing a like reaction, in the end accustomed themselves to the unexpected illumination and behaved almost in a normal manner.

Once outside of the hive, however, the impulse is to follow the light. Von Buttel-Reepen (1907, pp. 467-468) installed a hive of *Trigona* (*Plebeia*) *mosquito* variety *emerina* Friese in a space between an outer and an inner window. The imprisoned bees flew towards the light represented by the outer pane and, encountering this barrier, crawled laboriously about it without finding their way back to the nest. However, after three or four days a number of the bees had learned to fly within the narrow space between the two

windows and, overcoming the attraction of the light, to return to the flight hole. He felt this was very satisfying evidence of the ability of *Trigona* to learn, and Lutz, too, in the course of his experiments had convincing proof that stingless bees are quick to master shifting environmental conditions surrounding their nest entrance (Lutz, 1941, pp. 273-275), an account of which follows.

RECOGNITION OF THE NEST ENTRANCE AND THE VISION OF STINGLESS BEES

A highly interesting experiment was conducted by F. E. Lutz on Barro Colorado Island, Canal Zone. A nest of *Trigona* (*Tetragona*) *nigra* variety *paupera* (Provancher) was located in the wall of the laboratory building on that island, and the bees made their exits and entrances through a small hole in one of the boards on the outside of the wall. Lutz prepared a series of cards each with a hole at the center that corresponded in appearance with the hole through which the bees had access to the nest. But except for the hole that was common to all of the cards, each card had either an individual pattern or, if the same pattern, then a different combination of paints, limited however, to plain white, ultraviolet white, and black. To the human eye the paint that reflected plain white could not be differentiated from the paint that reflected ultraviolet white, for ultraviolet is, of course, beyond the color perception range of the human eye. A card having a pinwheel-like design composed of black and ultraviolet white segments alternating with one another looked for all the world like the card with the duplicate of the pinwheel-like design composed of black and plain white segments alternating with one another. A casual glance would have pronounced them the same and it would have failed to differentiate, too, between the many other pairs of cards in which the design of one duplicated the design of the other except that the whites used reflected in the one case plain white, in the other case ultraviolet white, or had varying combinations of these paints. But although the human eye was tricked into believing the cards the same, the bees knew the difference.

Lutz would place a given card over the nest entrance, with the hole of the card occupying

the position of the flight hole. Arrayed above it and below it and to the right and left of it were other cards of the varied series (a total of 25 cards) all united into a solid square, five cards in length and five in width (pl. 2, figs. 2, 3). The card over the nest entrance was left in place so that the bees might be educated to associate it with the portal of admission; the others were shifted frequently, so that there might be no fixity of design except for the constancy of the significant card, thus preventing the bees from associating the location of the nest with the position of the cards in general. After the bees had come to think of their nest entrance in terms of the significant card, the final test was made, but let it be related in Lutz' own words:

"A fresh card with the nest pattern but with no possibility of the nest odor on it was put on the wall but not at the right place. A card looking to us just like it but having a different pattern in ultraviolet was placed so that its hole was at the entrance to the nest and cards with other patterns were arranged near these two. The incoming bees flew to the right ultraviolet pattern in the wrong place and were much disturbed at being unable to get into the nest through the hole in the center of that pattern.

"Repeated experiments of the same sort seemed to demonstrate completely that these wild bees not only could distinguish between plain-white and ultraviolet-white but that they remembered the distinction and used it in such an important matter as finding the entrance to their nest" (Lutz, 1933, pp. 1-26; 1941, pp. 273-275).

Sapper (1935, p. 185) one time observed stingless bees flying persistently at the very level where formerly had been their nest. The tree in which the nest was located had been felled and the nest lay on the ground, but according to Sapper the bees were unaware of its presence. From this he drew the conclusion that their vision was of limited range. A similar instance of futile hovering at the precise level of the old nest site after the tree had been felled is recorded by Hughes (1933, p. 19), and it is possible the reference is to *Trigona*. Speaking of conditions in the region about Lake Bangweulu, located in the middle of the high tableland known as Tanganyika Plateau in central Africa, Hughes stated that,

when a tree is felled because a bees' nest is inaccessibly high in the tree, "bees coming home loaded, hover and circle pathetically in the empty air at the exact spot where the nest was before the tree was felled; gradually a large swarm collects." In this instance, at least, the felled tree was far removed from the spot where the bees were hovering and the nest itself possibly so mutilated that it was no longer recognizable. The cases cited by Sapper and Hughes do indicate that the bees had a strong locality sense, whatever be the conclusions as to their vision.

It was the contention of Girard (1875, p. 571) that the vision of at least *Melipona fasciata* variety *scutellaris* Latreille was better than that of *Apis* based on his personal observations.

WAX PRODUCTION AND A DISCUSSION OF THE ROLE OF THE MALE

The wax producing glands are differently distributed in the three main families of the social bees, although the abdomen is in all cases the seat of these organs. In the Bombidae the wax is secreted both ventrally and dorsally, in the Apidae only ventrally. It is generally stated that in the Meliponidae the wax issues only dorsally. That the wax scales are produced dorsally in the stingless bees there can be no dispute; the only possible doubt may be as to whether sometimes they are not also produced ventrally. Spinola (1840, pp. 118-127, 139, pl. 2) believed he had located the seat of a wax producing gland on sternites 2 to 6, thus assigning a ventral origin to the scales, while H. von Ihering (1886, p. 184) claimed that "Poorly developed ventral wax-producing organs seem to occur in many *Melipona* and *Trigona* in addition to the dorsal wax-producing organs." But, as Dreyling pointed out (1905, p. 316), von Ihering subsequently convinced himself that wax emission proceeded only from the dorsal abdominal segments.

The first European apparently to see wax exuding from the dorsal segments of the abdomen of stingless bees was F. Poey (1852, p. 161) but, although he compared the waxen lamellae to those produced by the honeybee in color, size, and consistency, he was seemingly completely misled in his interpretation of them and, instead of reaching what would

appear to be the obvious conclusion, he suggested that the lamellae were waxy particles derived from the bark of certain plants or from the surface of leaves. Indeed, he went a step further. He stated (1852, pp. 160-161) that stingless bees do not exude wax but manufacture it by drenching bits of resin with a fluid consisting of regurgitated pollen. He even advanced eight supporting reasons to justify this fantastic conception. Even 21 years later Hannemann (1872, p. 207) claimed that the wax of stingless bees was of vegetable and not of animal origin, an opinion pronounced on the very eve of Drory's discovery.

It was Drory (1873c, p. 173; 1873d, p. 60; 1874, p. 285) who, although not the first to witness the thin whitish wax scales issuing from the body of a stingless bee, was the first to interpret correctly the phenomenon. Drory thus recorded his experience: "After several weeks in which I had vainly sought how and where the bees sweat out or eject thin wax, I saw a *Melipona marginata* in which I believed to behold wax issuing from the mouth as claimed by Mr. Huber. I held her between my fingers and, as in turn I released her, I noticed four fine small longish white transparent scales which had remained behind. As I had clasped the bee only by the wings, I could have rubbed against her only dorsally. I convinced myself that it was indeed wax, for it melted very readily and diffused a wax-like odor. Now there was set in motion an examination of all the colonies and after some hours I had proof that all *Melipona* and *Trigona* emit wax between the dorsal segments of the abdomen, which, in the form of a small scale of whitish color similar to that of the honeybees, they scratch off with the hind legs and chew and fashion with their mandibles."

According to Drory the scales issue from five of the tergites. F. Müller (1874a, p. 309; 1874b, p. 102; 1875, p. 297) speedily confirmed independently Drory's observation of the dorsal origin of the scales and indicated that the same segments participate in the production of wax that function in this way also in the honeybee, an observation likewise recorded by his brother (H. Müller, 1875b, p. 42). In the honeybee the wax emitting organs are situated on the sternal plates of the last four visible segments of the abdomen,

each of these segments being equipped with two of these organs or a total of eight. In the opinion of Silvestri (1902b, p. 167) tergites 2 to 5 participate in the production of wax.

Dreyling, who made a comparative study of the wax producing glands in the social Apoidea (1905, pp. 289–326), found on the basis of his examination of specimens of *Melipona quinquefasciata* Lepeletier that the best developed scales were seemingly always on the last four tergites. From the second tergite he was able to obtain as a rule some wax but not comparable to the quantity on the subsequent tergites. On the other hand, it was Dreyling's conclusion that the first tergite participated at best to only a very slight extent in the production of wax.¹ Bischoff (1927, p. 286) has by implication deprived the first segment even of this inconspicuous role, listing as main wax producers the four apical tergites, with tergite 2 contributing less actively than tergites 3 to 6. This is the impression one derives also from Deegener (1912, p. 41). Wheeler (1928, p. 99) limited the production of wax in the case of the Meliponidae to the dorsal side of segments 2 to 4. Salt (1929, p. 442) noted wax plates coming from under tergites 2 to 4 of young workers of *Trigona* (*Cephalotrigona*) *capitata* variety *zexmeniae* Cockerell. According to Imms (1931, p. 45) the wax is secreted "between the dorsal shields of the second to fourth abdominal segments." Schulz (1905c, p. 141) observed in the case of *Trigona* (*Partamona*) *testacea* variety *cupira* F. Smith that wax was issuing between the interstices of the last three dorsal segments. In a large series of *Trigona* (*Partamona*) *testacea* variety *testacea* (Klug) that I have examined are several specimens that have wax scales attached to the extreme apex of tergite 4, these scales being coextensive, or nearly so, with tergite 5. It is my impression that these scales must have been produced by the wax glands of tergite 5 and that they were made fast to the hairy apex of tergite 4 through the pressure of one tergite upon the other as the scales moved downward from

the concealed basal region of tergite 5 towards the exposed apex of tergite 4. I am inclined to believe accordingly that the tergites involved in wax production extend apicad beyond tergite 4, as claimed by Dreyling and others, but it is possible, in view of the range of observations and inferences cited, that in some species there is a fuller participation of certain wax producing glands than in others.

It is by the younger adult Meliponidae that wax is produced; in the older adults the wax glands degenerate. These glands bear a surprising resemblance to those of the honeybee, in all except location, being alike in both groups in structure as well as in development (Dreyling, 1905, pp. 319–321). In the honeybee other physiological developments, such as the production of royal jelly, precede the production of wax. But in the stingless bees wax production would seem to begin very early, for Schulz (1905c, p. 141) noted the wax scales even on callows of *Trigona* (*Partamona*) *testacea* variety *cupira* F. Smith, and this accords with my own observations on the typical variety of this species. Drory (1873c, p. 173) similarly recorded the emission of wax from callows of what may have been *Trigona* (*Tetragona*) *nigra* variety *paupera* (Provancher).

Of special interest is the fact that, although in the honeybee it is the worker only that produces wax, and in the bumblebee only the worker and the queen, among the Meliponidae all three castes are said to have this capacity (Wheeler, 1928, p. 99). It was Drory who first observed and made known this alleged ability of the male meliponid, so at variance with the limited achievements except for fertilization evidenced by the male of bees in general. It was natural, therefore, that Drory should proceed to the conclusion that within the nest the male meliponid participates with the worker in the tasks of construction (1873d, p. 60). After mentioning the capacity of the male to secrete wax he added, "It is evident then that the males labor as do the workers in the interior of their dwelling in contributing to the construction of the jars of honey and the nest of the brood." Later (1877, pp. 144–145) Drory is even more emphatic: "Males of the honeybee do not work; they are not even capable of working. Those of the Meliponidae not only

¹ In addition to studying many specimens of *Melipona quinquefasciata*, Dreyling had access to a few specimens of different species of *Trigona* and found in all of them that the glands were dorsal in location and well developed on segments 2 to 6 (1905, p. 322).

work but, like the workers, they secrete wax from the dorsal segments of the abdomen."

One would give much to know whether Drory actually observed male bees engaged in building or whether he assumed that they would be thus occupied in view of the fact that nature, according to his observations, had endowed them (alone among bees of their sex) with the capacity for producing building materials. His statement of 1873 seems to be based on inference, that of 1877 presumably on observation, for in that later statement he appears to imply that the wax production is the more astounding of the male's accomplishments. On the other hand, other students have been skeptical regarding the building activities of the drone. Girard (1879, p. 708) early expressed the wish that others might confirm the observations of Drory. Bischoff (1927, p. 286), while assenting to the belief that the male produces wax, went on to say that participation of the male in the activities of the nest has not as yet been observed. Silvestri (1902b, p. 167) dismissed the idea that any caste other than the worker participated in pollen and honey gathering.

The alleged wax production of the male (and also of the queen) is in itself so startling that one is inclined to pause and wonder whether Drory could have been mistaken.

One of the things that is puzzling is the possible lack of adequate equipment both in the male and in the queen for the removal of the wax plates. Spinola (1840, pp. 121-127, 139, pl. 2) incorrectly interpreted the function of the auricle on the hind metatarsi of the honeybee, which he believed (and he was not alone in the belief) to be a pick with which to remove the wax scales, but his theory that the tibial comb of the meliponid bees is a wax remover has at least not been vigorously challenged. This function of the tibial comb is accepted as a fact by Blanchard (1868, p. 463), who is quoted, apparently with approval, by Holmberg (1887, p. 274). With like approval H. von Ihering (1903, p. 259) cited the statement of similar purport made by H. Müller that the tibiae at their apex "are provided with a comb of long curved teeth of chitin, which presumably is used to extract the tiny plates of wax." The only qualification that von Ihering makes is that the credit for the discovery of this function

properly belongs not to F. Müller, as alleged by H. Müller, but to Drory, whereas it was really Spinola who first called attention to this putative use of the comb. Peckolt, too, expressed the opinion (1894, p. 87) that the tibial comb probably served for the removal of the wax, and the same is affirmed by Marshall (1898, p. 131). Girard (1879, p. 706) was a little more cautious, assigning this role to the tibiae instead of just the comb of the tibiae.

Certainly here is a weighty total of opinion that cannot be lightly challenged, and the comb in question seems structurally so well adapted to the purpose for which it allegedly exists that one is strongly inclined to accept the interpretation of this aggregate of authors, the more so as several of them seem to have reached their conclusions independently. On the other hand, if this comb really has the function assigned to it, how shall we account for its absence in the male and in the queen, which, if they be wax producers, are in the predicament of being burdened with a sticky adherent substance (and a useful one at that) yet without visible means of getting rid of it? Or is the pectinate implement anteriorly and externally on the apex of the tibiae of the worker not a wax remover after all? Or is Drory's impression that the male produces wax fallacious?

In this connection one cannot help wondering, too, how *Lestrimelitta* manages things. *Lestrimelitta* resembles other stingless bees in lacking this comb in the male and in the queen but is utterly unique in lacking it also in the worker. Even those who accuse *Lestrimelitta* of living by robbery alone, indicate nevertheless that she makes her own new internal arrangements in the nests she has usurped (Fiebrig, 1908, pp. 374-375) and that rather implies the ability to produce wax and to remove it at will.

Notwithstanding the fact that Spinola's interpretation of the use of the anteriorly placed tibial comb of *Melipona* and *Trigona* bees was predicated on the mistaken belief that, like *Apis*, the Meliponidae exude their wax ventrally instead of dorsally, it should not be hastily dismissed. Some use this anterior comb would seem to have other than that of being purely ornamental, for this comb is lacking in the queen, and the queen

in so many ways evidences a degeneration or loss of structures vital in the activities of the worker that, when a given structure has disappeared from her anatomy, one is inclined to regard it as but another evidence of the desuetude of some correlated function.

Yet I confess the tibial comb (that is, the comb that is placed anteriorly on the outer side of the apex of the joint and not the dense row of spines or spine-like hairs along the apical edge of the inner side of the joint) whatever its function, if any may be, does not seem ideally adapted for wax removal from the dorsal side of the abdomen. To reach the wax scales the hind leg would have to undergo considerable contortion. It would have been so much more convenient to have the comb on the under side of the tibiae rather than on the upper side in view of the dorsal location of the wax secreting glands. It seems more probable, therefore, that some other part of the hind leg has the function of wax removal.

Possibly it is the row of spine-like hairs inward along the apex of the hind tibiae that is used in wax removal. These, as is the tibial comb, are characteristic of the worker rather than the male. Or it may be the brushes on the inner face of the hind metatarsi that are called upon to play this role. These brushes are well developed in the worker but are also fairly stiff and resistant in many males.

Only on the assumption that the tibial comb and the tibial spines are not involved in the removal of wax plates does it seem to me even remotely justifiable to hold to the belief that the male like the worker engages significantly in wax production, and even with such a mental anchorage I am frankly skeptical.

Rayment (1932a, pp. 188-189; 1935, pp. 516-517) believed the tibial comb was evolved from "the coarse type of calcar" of certain ground dwelling bees. "As the necessity for excavating gradually disappeared," conjectured Rayment, "the long 'teeth' of the tibial calcar became so slender that they finally separated into distinct chitinous spines, the majority of which are simple, a few are biforked and an odd one triforked, thus demonstrating in no uncertain manner its remarkable origin." However, among stingless bees of sub-

terranean habit, a rake for scooping out soil might still have its uses provided Rayment is right that this implement of the bees is a derivative from a digging tool.

But to return to our males and their alleged wax producing capabilities. Not only do the males lack the tool that Spinola associated with the removal of wax; I have found that the usually concealed basal part of the tergites of some species (the area in which the wax glands are located) shows a difference of sculpturing in the case of the worker and of the male. Thus in the subgenus *Paratri-gona*, for instance, this area, usually overlapped by the preceding tergite, tends to be smooth and polished in the worker, while in the conspecific male it is frequently sculptured, at least lightly. One cannot help wondering whether the greater smoothness of this surface in the worker is not in some way associated with the smoother and more efficient delivery of the wax.

Even if the male should be able to produce wax and had the further capacity of removing it, it is still not clear how the wax could be successfully manipulated. In no species does the mandible of the male seem so well shaped or equipped for wax manipulation as in the conspecific worker, while the mandible of many males, at least, seems quite unfitted for the task.

The comments I have made suggest doubt regarding the wax producing capacity of the male. If such a capacity exists, it would seem, at least, that it must be of more limited application than in the worker. I personally have never seen wax scales issuing from the dorsal surface of the abdomen of the male, but a positive observation, like that of Drory, has more validity than a mere absence of observation of the phenomenon. It is to be noted, too, that Silvestri (1902b, p. 167) affirmed that males as well as workers among the stingless bees produce wax, but it is not clear whether his statement rests on field observations or merely repeats an unchallenged statement.

There is, of course, the possibility that Drory mistook for the male some other caste of the colony. In this connection it is perhaps worth mentioning that he found no males (1872b, pp. 159, 190) in a colony of *Melipona fasciata* variety *scutellaris* Latreille, although

the presence of virgin queens, of which Drory took note, makes it seem likely that males were also on hand. Even more significant is the fact that in what I think was probably a colony of *Trigona* (*Tetragona*) *nigra* variety *paupera* (Provancher) he interpreted the callow specimens of white abdomen as true workers, while he designated the individuals of black abdomen as possible males. Such an attempt to sort worker and male not by differences of structure but on the basis of a character that is probably merely indicative of the age of the individual permits the conclusion that up to 1872, at least, Drory did not have too clear a notion of the character of the male of stingless bees.

In a later paper (1874, p. 285), in which the production of wax by the male is stated with confidence, Drory does, however, list characters of the male which are definitely indicative of that sex, such as the cleft tarsal claws, the 13 joints of the antennae, the narrower face of the male and its white color (a character of only limited application). He must, therefore, presumably have been able to discriminate between workers and males. As in the case of the discovery of the wax producing activities of the worker, so in the case of the discovery of the alleged wax producing capacity of the male, it was *Melipona marginata* Lepeletier that furnished the evidence. Drory's report of the discovery is worth citing in full:

"I had neglected the male, for I assumed that, like the male of the honeybee, they were unfit for labor. Then one day, as I wanted to take out a worker of 'Urussu mirim' [*Melipona marginata* Lepeletier] in order to show a visitor how the bee produces wax, I grasped by mistake a drone; before I released the drone I showed the gentleman the hind legs, which are hardly to be differentiated from those of the workers, a condition that always astonished me. Then, all of a sudden I beheld wax scales on the back; at first I did not want to trust my eyes, but dragged out presently one male after another, and of 43 there were 37 that were bedecked with wax scales on the back. Not satisfied even yet with this, I examined two colonies of 'Abelha urussu' [*Melipona fasciata* variety *scutellaris* Latreille] with like success; in a word, I was able to establish with certainty that the males as

well as the workers are capable of producing wax, and take part in domestic activities.

"Whether likewise they fly forth in order to gather honey and pollen, I have not yet been able to determine."

Drory's statement is full and emphatic with respect to the capacity of the male stingless bee for wax production, and it requires hardihood to cast doubt upon it. A skeptic, however, might wish to have clarification on the claimed resemblance between the hind leg of the worker and the hind leg of the male of *Melipona marginata* Lepeletier. Under the microscope, at least, the hind legs of these two castes of *marginata* appear rather dissimilar, much more dissimilar, for instance, than is the case in some other *Melipona* such as *beecheii* Bennett, *interrupta* Latreille, and *quinquefasciata* Lepeletier, in which the shape of the hind leg of the male rather closely approximates that of the worker (Schwarz, 1932a, pl. 5). Even viewed with the naked eye, the hind legs of a *marginata* male look different from the hind legs of a *marginata* worker.

This raises the further speculation whether it was with the naked eye or through a magnifying glass that Drory made his observations. To this question his text gives no certain answer. One likes to think that a lens of some kind was employed; but in case the observations were made on living specimens (as seems to be the fact) and with the naked eye (and we may recall that Drory intimates that he was at first unwilling to trust his eye) there is still the possibility that, as in the case of the putative *Trigona* (*Tetragona*) *nigra* variety *paupera* (Provancher), where Drory interpreted as males what were with greater likelihood workers, a similar mistake of interpretation may have occurred in the case of *Melipona marginata* Lepeletier and *Melipona fasciata* variety *scutellaris* Latreille.

So careful an observer as Salt, when examining nests of *Melipona interrupta* variety *salti* Schwarz and of *Trigona* (*Cephalotrigona*) *capitata* variety *zeuxmeniae* Cockerell, commented to the effect that certain workers of these species were emitting wax, but in neither case does he mention males as being similarly engaged (Salt, 1929, pp. 435, 442).

What shall we say regarding the further claim that the males not only produce wax

but aid in construction within the nest? Now and then I have seen males, more particularly within the subgenus *Trigona*, that bore some adhesive material on their hind tibiae. Such males may have simply blundered into something sticky in wandering about the hive and thus inadvertently and undeservedly acquired the earmarks of industry. Many of the 417 males that C. D. Michener collected from a large nest at Juan Mina, Canal Zone, were thus besmeared on the hind tibiae, but the fact that these males almost invariably bore other evidences of untidiness (sometimes it was the head, sometimes the thorax that was similarly gummy) leads me to believe that little significance can be attached to these manifestations. Indeed two of the males even had what seemed to be pollen caked over their faces and plastered over part of one of their tibiae, but such an unequal distribution, at variance with the balanced loads of the foraging worker, hardly permits one to conclude that these two individuals had been emulating the example of their sisters in exploring the floral pasturage afield.

The males of some subgenera seem better fitted from the standpoint of their structure to act as hod carriers than are other males, and males of the subgenus *Trigona* with their equipment of plumose hairs, more or less in conformity with the condition in the worker, seem moderately favored by nature for constructive tasks. Against this must be weighed the fact that such activities on the part of the male are at variance with what is generally known regarding that sex in the Apoidea, and the further fact that it is hard to believe that within the Meliponidae such a practice as the slaughter of the drones would have come into existence if it were not a provision of nature for getting rid of a group of only limited function after that function (the fertilization of the queen) had been achieved.

Rayment, who made observations on Australian stingless bees, affirmed (1935, p. 514), "The male's sole function is the fecundation of the young 'princesses.'" McKeown (1942, p. 203) expressed the like thought, "The little male bees exist with the sole function of fertilizing the females." Another student of the stingless bees, H. von Ihering,

who had excellent opportunity for making observations and who has shed much light on their biology, had previously come to much the same conclusion as Rayment and McKeown. The role of the male, von Ihering indicated (1903, p. 256), appears to be exactly the same in the domestic setup of the Meliponidae as in the honeybee. H. von Buttel-Reepen (1903a, pp. 142-143; 1915, p. 80), on the other hand, assumed that the male to some extent participated in the construction of the nest and accepted the contention that this sex is capable of producing wax. One wonders whether von Buttel-Reepen's conclusion regarding the wax secreting capacity of the male was based on observation. It might have been, for von Buttel-Reepen had some imported hives of stingless bees (1915, p. 143).

I am inclined to be cautious in accepting the statement of the functions of the male as interpreted by Castets (1908, p. 53), because his article contains other statements that evince incomplete knowledge. However, as an extreme view regarding the efficiency of the male of *Trigona* (*Tetragona*) *iridipennis* F. Smith, Castets' statement is quoted herewith: "They [the males] know how to take their food themselves, how to arrange the different materials brought by the workers, and, when it is a question of attacking an intruder, they are often the first and most determined."

Both the wax production of the male and the alleged participation of the male in the household activities of the hive should be further investigated in order to clarify these divergent interpretations.

PROTANDRY

The appearance of males would seem to be intermittent, not continuous, with gaps during the year when no members of this sex are represented in the colony. Tomaschek (1879, p. 587) could discover no drones in the colony he interpreted as that of *Trigona* (*Paratrigona*) *lineata* (Lepeletier), nor could Schulz (1904b, p. 819) find males in a nest of *Melipona fasciata* variety *scutellaris* Latreille. In several nests examined by H. von Ihering there were no males. This sex was not represented, for instance, in a nest of *Melipona marginata* Lepeletier examined by von Ihering.

ing (1903, p. 197) on February 16, or in a nest of *Trigona* (*Partamona*) *testacea* variety *cupira* F. Smith opened by the same investigator (1903, p. 209) on January 29, or in a nest that he recorded as that of *Trigona dorsalis* F. Smith [but that more likely is to be ascribed to *Trigona* (*Scaptotrigona*) *postica* Latreille or a near relative] which was obtained on March 17. Two additional nests of the last mentioned species were examined by von Ihering on April 12 and on August 28, respectively, and in neither were males found (1903, p. 215). All of the nests regarding which he reported were from southern Brazil, yet in at least five different months of the year (and not all of these falling within the colder period) males were lacking in the case of this nest or that. In Colombia a nest of *Melipona favosa* (Fabricius) examined by Salt (1929, pp. 437-438) was devoid of males, as was a nest of *Trigona* (*Trigona*) *amalihea* (Olivier) examined by the same investigator (1929, pp. 438-441).

There would seem no reason to doubt that there are times when the hive is devoid of males, but are the occasions of the appearance of males haphazard or are these appearances correlated with the emergence of the virgin queens, and do the males leave their cells somewhat before their royal sisters or half-sisters in conformity with protandry so general among the Apoidea? I am tempted to think protandry is the prevailing pattern, even though the literature contains some instances that may be interpreted as pointing to the contrary. A great many of the seeming exceptions, however, can be explained away. In certain *Melipona* colonies adult males have been noted but no virgin queens, and the analysis of such nests has frequently included the comment, "no royal cells" (a phrase often occurring in H. von Ihering). To the unwary this tends to convey, doubtless unwittingly, the impression that males appear independently of the young queens. Quite the contrary may, however, be inferred when emphasis is given to the fact that throughout the genus *Melipona* so far as known there is no differentiated royal cell; the queens emerge from cells that do not differ from those occupied by the worker or by the male. Accordingly, it is quite as logical to assume in the case of nests where males are present without

visible accompaniment of virgin queens that some of the immature bees in these undifferentiated cells will emerge as virgin queens as it is to adopt the belief that none of them will so emerge.

The reverse of the situation noted for *Melipona* manifests itself in the literature of *Trigona*. In *Trigona* the royal cells are conspicuous owing to their size, while the cells containing the males and the workers cannot be differentiated from one another. Hence the inclination is to record the number of royal cells, thereby imparting the information that young queens are an early prospect, and at the same time to lump the other cells indiscriminately as brood cells because they give no external evidence of the sex or caste of the occupant. Yet it is, of course, quite possible that in those brood cells are pre-adult males, sealed from view, that are of a more advanced stage of development than that attained by the inmates of the royal cells. As a result, in cases where royal cells of *Trigona* are reported but no mention is made of males, I am of the opinion that unobserved developments within the undifferentiated brood cells may be taking their course in conformity with protandry, and that this possibility renders of little relevance reports based on a study of the cells merely from the outside.

In fact, the validity of this line of reasoning is well illustrated in connection with a species that H. von Ihering (1903, pp. 211-216) recorded as *Trigona dorsalis* F. Smith but which more probably was affiliated with *postica* Latreille. On October 5 a nest of this form was examined that contained royal cells, but no mention of males was made because the cells in which doubtless they were lodged were not different from those of workers. In a nest of the same insect examined less than two weeks later (October 17) there were both males and virgin queens as well as a queen cell from which the occupant had not yet emerged.

Definitely supporting the view that protandry is of normal occurrence are three instances in the records of H. von Ihering: one of a nest of *Trigona* (*Trigona*) *fulviventris* variety *guianae* Cockerell observed on October 19 (1903, pp. 217-219), the second of a nest of *Trigona schrottkyi* Friese examined on September 18 (1903, pp. 231-232), the third

a nest of either *Trigona* (*Scaptotrigona*) *postica* Latreille, identification of Friese, or *Trigona* (*Scaptotrigona*) *bipunctata* Lepeletier, identification of Schrottky, collected July 2, 1903 (H. von Ihering, 1912, pp. 43-44). In these nests adult males were noted as well as queen cells. In a colony of *Trigona iridipennis* F. Smith, there were workers, males, and a gravid queen but as yet no princesses (Friese, 1914a, p. 52).

A case possibly of similar character is that communicated to me by Mr. R. G. Donald with reference to a nest of *Melipona fasciata* variety *trinitatis* Cockerell which he examined on Trinidad Island, British West Indies, on September 18, 1945. From it he took a sample lot of the inhabitants, among which he found four fully colored males and five males that were of light color and presumably, therefore, recently emerged. After an interval of a week or more, during which he was prevented from studying the nest, he again examined it and on this occasion opened all the brood cells. "Several more males were thus procured, as well as one virgin female, which, although developed, was dead." It is not to be ruled out, of course, that there were virgin queens in the nest at the time the sample lot was taken, but on the basis of the available evidence the males had emerged, the lone virgin queen had not.

What seems a convincing case of protandry is cited by F. Müller (1878, p. 229). A nest of "gurupú" (presumably *Melipona schencki* Gribodo) that succumbed after a few weeks of domestication was examined with respect to its nest population, which consisted of 294 workers (none of which had as yet reached their full coloration), 59 males (nearly all of which were fully colored), and 21 females (some of which had not yet emerged from their brood cells). Here the sequence of emergence would seem to have been almost certainly males before virgin queens.

Yet even though protandry would seem to be the prevailing pattern, it evidently does not work with complete precision, there being cases of retarded appearance of some males or accelerated emergence of some queens. Thus Salt (1929, p. 435) noted on July 30, 1927, in a nest of *Melipona interrupta* variety *saltii* Schwarz about 15 young females and

an undetermined number of males, but within four days thereafter there emerged five additional females and also seven males.

Protandry seems possibly to be indicated in a colony of *Trigona* (*Cephalotrigona*) *capitata* variety *sexmeniae* Cockerell which Salt (1929, pp. 441-442) examined on September 27. Here, in cells indistinguishable from those of the worker and scattered indiscriminately among the worker cells in the proportion of about one to 12, were maturing male bees. Two queen cells were also noted, one of which contained a pupa, the other a larva. It should be mentioned, however, that, in addition to these immature members of the royal caste and to the queen mother, there was a non-physogastric female in the nest, possibly a survivor from an earlier generation.

Virtually in the proportion of one to 12 were the males compared to the rest of the population in a large nest of *Trigona* (*Trigona*) *corvina* Cockerell, weighing 69 pounds. This nest was collected by C. D. Michener in Juan Mina, Canal Zone, on April 27, 1945. The recovered nest population consisted of 6529 bees, which Michener estimated at more than 90 per cent of the colony. A number of bees were rejected because honey dripped upon them from the broken honey containers damaged in the course of opening the nest. However, 5201 specimens were sent me, and an analysis of these showed 4782 workers, 417 males, and two virgin queens. The proportion of males to workers was as one is to 11.47. The males, in other words, constituted about 8 per cent of the recovered population sent me. The physogastric queen, Michener reported, was "very likely present but lost in the great bulk of sticky, honey-covered pieces of wax."

Departing only slightly from the proportion of males in the nest referred to in the previous paragraph is that which obtained in a nest of *Trigona* (*Trigona*) *fulviventrís* Guérin kindly sent me by Dr. T. C. Schneirla from Huixtla, Chiapas, Mexico. The nest, which was collected on January 27, 1945, contained at least 3039 adult bees, of which on examination I found 2748 to be workers and 290 to be males. Thus the males were in the proportion of one to 9.48 workers, or a little over 9.5 per cent of the total population. There was one physogastric queen, but no

virgin queens were noted among the nest occupants sent me.

As the function of protandry in the economy of nature is to assure the presence of males when the opposite sex appears upon the scene, instances of the presence simultaneously of males and virgin queens in a nest do not preclude the possibility that, if an earlier inspection of the nest had been made, males would have been noted without accompanying virgin queens. The simultaneous presence in the nest of both males and young adults of the royal caste was noted by J. M. Pérez (1895a, p. 273; 1895c, p. 125) in the case of *Melipona fasciata* variety *scutellaris* Latreille; by Du Buysson (1901a, p. 104; 1901b, pp. 153-155) in the case of *Melipona beecheii* Bennett; by H. von Ihering (1903, p. 195) in the case of *Melipona quadrifasciata* variety *anthidioides* Lepeletier on August 28 and in the case of what H. von Ihering (1903, p. 212) designated *Trigona dorsalis* F. Smith (more probably it was close to *postica*) on October 17; by Salt (1929, pp. 434-437) in the case of *Melipona interrupta* variety *salti* Schwarz on July 30. Three queens and a limited number of males were noted by Schulz (1905c, p. 140) in a nest of *Trigona* (*Partamona*) *testacea* variety *cupira* F. Smith. Schulz toyed with the idea that these queens might be gravid, but the photograph he supplied of one of them seems to me to indicate a virgin condition. There were no royal cells in the nest examined by Schulz. There is before me nest material of a form close to *Trigona* (*Scaptotrigona*) *bipunctata* Lepeletier, which includes five virgin queens and 280 males. The nest was collected on January 26 at Nueva Italia, Villeta, Paraguay, by Pedro Willim. I am informed by R. G. Donald that in a nest of *Melipona favosa* variety *favosa* (Fabricius) opened on October 2, 1945, there were found "1 gravid queen, 28 virgin queens, and numerous males." In addition to sending me specimens of all casts from this nest of *favosa*, Donald also kindly submitted to me specimens of *Lestrimelitta limão* (F. Smith) which he collected from a nest on July 26, 1945. The material sent me included, in addition to workers and males, also one gravid queen and two virgin queens. It is worthy of note that, although there was a gap of about three months between the dates of examination

by Donald of the nests of the two species mentioned, in both cases males and virgin queens were present. The nests of both of these species were collected on Trinidad Island, British West Indies.

At least tending to indicate the interdependence in the emergence of males and virgin queens even if they do not directly support the evidence for protandry are those cases where there is simultaneous absence of males and of their royal sisters or half sisters from the hive. Nests of "*Trigona dorsalis*" examined by H. von Ihering (1903, p. 215) on April 12 and on August 28, respectively, lacked evidences of the presence of young queens as well as of males. H. von Ihering (1911, p. 132) noted that in a nest of *Trigona* (*Hypotrigona*) *muelleri* Friese there were neither males nor royal cells. No mention of royal cells was made by Stadelmann (1895, pp. 615-621) in describing a nest of his *Trigona erythra* variety *togoënsis* from Africa, and, in spite of careful search, no males and apparently no young queens were found among the inhabitants of the nest. Absence of males and unfertilized females of the royal caste is indicated by Du Buysson (1901a, p. 106; 1901b, p. 155) in the case of a species he interpreted as *Trigona lineata* (Lepeletier). In a small nest of *Melipona marginata* Lepeletier (it consisted of but a single completed comb) neither males nor young queens were observed by Schulz (1905a, pp. 199-204), nor did that writer find among the surviving population of a nest of *Trigona* (*Plebeia*) *mosquito* variety *emerina* Friese any representatives of either of the sexual forms (1905a, p. 252) nor were there royal cells. Notwithstanding a careful search of the nest, Schulz failed to find any members of the royal caste or males in a colony of what he designated *Melipona scutellaris* Latreille (1904b, pp. 818-819). In a nest of *Melipona favosa* (Fabricius) examined by Salt (1929, pp. 437-438) there were evidently no virgin queens, for Salt mentioned only the physogastric queen and from the proportions of head and thorax concluded that the virgin queens must be smaller than the workers. He then went on to say, "Males were not seen." A colony of *Trigona* (*Trigona*) *chanchamayoënsis*, new species, that W. Weyrauch obtained at La Merced, Peru, on March 2, 1940, contained

only one member of the royal caste, a physogastric individual. Of royal cells there was no more evidence than there was of virgin queens. Weyrauch sent me somewhat more than 850 bees from this nest, but among them (although each was individually examined by me) there was not a single male.

Recently I secured through the courtesy of Dr. T. C. Schneirla a colony of *Trigona* (*Trigona*) *amalihea* (Olivier) collected at Huixtla, Chiapas, Mexico, on January 18, 1945. Except for a single physogastric queen all of the remaining specimens sent me (an aggregate of 2075) proved on examination to be workers. Schneirla estimated that the specimens collected represented more than one-half of the total nest population. He instructed his field assistant to include all specimens of exceptional appearance, and there is little reason to suppose, therefore, that virgin queens, had there been any, would have escaped inclusion. The total absence of males among the nest population submitted supports the belief that this sex was not represented at the time the nest was collected.

The instance most disconcerting to the conception of protandry as well as to the notion that males appear recurrently from year to year and within each year is the report of J. M. Pérez (1895a, pp. 273-275; 1895c, pp. 125-126), who had under observation from the beginning of November, 1891, until the middle of October, 1894, "a little *Trigona* from Uruguay," from which he learned "some facts that were entirely unexpected." These "facts" were that (1) during the first year the colony produced nothing but workers, (2) during the second year the colony produced, in addition to workers, a single virgin queen, (3) during the third year several royal cells were constructed, although a parasitic disease, which overtook the colony, included among its victims the immature occupants of the cells as well as the adult bees. The significant thing in Pérez' account is not only the progressive increase from year to year in the number of queens but the total absence, during this long period, of observed males. One hesitates to challenge the conclusions of one who gave devoted observation to a colony over so long a period, and yet the observation is so unusual that

one wonders whether a mistake could have been made. We know that Pérez recognized the male in other colonies of bees; could he have failed to recognize it in this one? Unfortunately Pérez does not mention his colony by name. What he does indicate is that it was a small *Trigona*, and in the case of a small *Trigona* males and workers are not always readily differentiated in a living colony. Moreover, there is one phase in his account which furnishes a refuge for those who may wish to question the correctness of his interpretation. With reference to the first year of his observations he says: "Though I was every day on the watch, so to speak, for slightest differences that might appear in the shape and dimensions of the freshly constructed cells, and might lead one to suppose that a queen—or male—cell was being produced, I never noticed anything peculiar in the building operations, and never witnessed the emergence of any but workers."

Herein lies a possible error, for Pérez was looking for something that in all probability did not exist. Instead of basing his assertion regarding the absence of males on an analysis of the living specimens, it would seem from the above quotation that he probably drew his conclusions largely from the lack of differentiation in the structure and size of the brood cells. But in instance after instance it has been shown that, unlike the condition in the honeybee, stingless bees build cells of identical character for both male and worker. We have noted that in the genus *Melipona* even the royal cell is not differentiated. The probable uniformity of male and worker cells throughout the Meliponidae is strongly supported by the fact that, again unlike the condition in the honeybee, there is among the stingless bees no difference, or only a negligible difference, in size between adult worker and male. So it is possible, or one may be justified even in saying probable, that males did make their appearance in Pérez' colony during the period of his observation but that because of their similarity in appearance with the workers and his reliance on the size of the cell as a clue to the caste, he failed to recognize the males in the mixed population.

Pérez praised what he believed to be a maleless colony as a device of nature to in-

sure cross fertilization, but not only is there doubt in my mind as to the dioecious character of Pérez' colony, but it seems to me that we know too little about the mating of stingless bees to assume that such a one-sided development of a colony would assure fertilization. Possibly stingless bees mate, as does the honeybee, in open flight in the air, but other members of the social Apoidea—for instance, bumblebees—are thought to mate in the nest or have even been observed mating on the leaves and branches of trees (Lie-Pettersen, 1901, Bergens Mus. Aarbog, no. 6, pp. 3-10).

In passing it should be mentioned, too, that Pérez had under observation for some weeks a colony of *Trigona* (*Tetragona*) *clavipes* (Fabricius). A large number of males were noted but not a single virgin queen. Pérez did not comment on the presence or absence of royal cells, and one is left in doubt whether this is a case of protandry or an exception to it.

Another case that is somewhat disconcerting to the view that protandry is the standard order of things is the instance cited by H. von Ihering (1903, p. 194) of a nest of *Melipona quadrifasciata* variety *anthidioides* Lepeletier examined on February 7 in which as of that date there were neither young queens nor males. But some days later young

queens began appearing to the number of 14 to 16. These young queens were conspicuous because of their coloration, short wings, and other characters. Here, it would seem, is a case where the young queens emerged ahead of their brothers or half brothers, but it is just possible, too, that the males were overlooked, resembling as they do in coloration and size the conspecific worker and being much less sharply differentiated from the worker than is the queen.

It will be of assistance to tabulate by species and with date the nests that gave evidence of mature or maturing sexual individuals. In the list have been included those nests of *Trigona* that had royal cells but no adult males, on the assumption that in the undifferentiated brood cells males of a stage of development corresponding with, or more advanced than, that of the queens were represented. Similarly those nests of *Melipona* have also been included in which males but no virgin queens were observed, on the assumption that among the undifferentiated brood cells were some that would presently yield such queens. The tabulation has been confined to the nests observed by H. von Ihering (1903, pp. 187-235) because these have approximate geographic unity and are sufficiently numerous to be of aid for purposes of comparison:

<i>Melipona quadrifasciata</i> variety <i>anthidioides</i> Lepeletier	Sept. 14, 1900	Males
	Aug. 28, 1902	Males and virgin queens
<i>Melipona marginata</i> Lepeletier	Aug. 28, 1902	Males
<i>Melipona fasciata</i> variety <i>rufiventris</i> Lepeletier	Mar. 15, 1901	Males
<i>Trigona</i> (<i>Partamona</i>) <i>testacea</i> variety <i>cupira</i> F. Smith	Jan. 29, 1901	Royal cells
? <i>Trigona dorsalis</i> (probably <i>Trigona</i> (<i>Scaptotrigona</i>) <i>postica</i> Latreille)	Oct. 5, 1900	Royal cells
	Oct. 17, 1900	Males, virgin queens, royal cell
	Nov. 11, 1900	Royal cells
	Mar. 17, 1901	Royal cells
<i>Trigona</i> (<i>Scaptotrigona</i>) <i>tubiba</i> F. Smith	Aug. 31, 1900	Royal cells
<i>Trigona</i> (<i>Trigona</i>) <i>fulviventris</i> variety <i>guianae</i> Cockerell	Oct. 19, 1900	Males, royal cells
<i>Trigona</i> (<i>Trigona</i>) <i>ruficrus</i> (Latreille)	June 15	Royal cells
	Nov. 11	Royal cells
	Mar. 31, 1901	Royal cells
<i>Trigona</i> (<i>Tetragona</i>) <i>jaty</i> F. Smith	Aug. 28, 1902	Royal cells
<i>Trigona</i> (<i>Plebeia</i>) <i>molesta</i> (Puls)	Oct. 19, 1900	Royal cells
<i>Trigona schrottkyi</i> Friese	Sept. 18, 1902	Males, royal cells
<i>Trigona</i> (<i>Tetragona</i>) <i>mombuca</i> variety <i>subterranea</i> Friese	May 21, 1900	Royal cells

In this limited list of records there are as many as eight different months in the year in which royal brood was present either as an emerged insect or in process of development, with the probability strong that, where royal cells were present, there were also other cells harboring maturing males. Several of these months fall within periods of the year which belong to the fall or winter of the Southern Hemisphere. In some cases H. von Ihering regarded the presence of royal cells as unusual for the season. The nest of *Trigona* (*Tetragona*) *jaty* F. Smith examined on March 31 was alone among the nests studied on this date to evidence this distinction, but such dates as May 21 and June 15, which likewise appear in the above list, would also seem remarkable. The presence of males and virgin queens in a nest of *Melipona quadrifasciata* variety *anthidioides* Lepeletier on August 28, 1902 also prompted an attempted explanation by von Ihering (1903, p. 195). He called attention to the circumstance that June and July of the year in question were exceptionally mild and seemed to give promise of an early spring. J. M. Pérez (1895a, p. 273; 1895c, p. 125) recorded the presence in autumn, in a nest of *Melipona fasciata* variety *scutellaris* Latreille, of both males and queens, and he emphasized the incongruity of this occurrence by indicating that the entire colony shortly thereafter succumbed to cold.

Before closing this subject it is perhaps only proper to indicate that in the social Hymenoptera protandry is sometimes absent. Thus so excellent an observer as Rau (1929, Ann. Ent. Soc. Amer., vol. 22, pp. 668-669) found only queens and workers in a nest of the bald-faced hornet [*Vespula* (*Dolichovespula*) *maculata* (Linnaeus)] examined September 2, whereas during the next 30 days males to the number of 52 as well as queens to the number of 85 made their appearance. It would seem, therefore, that here is a case where the queens arrived on the scene (or at least some of them) before the males made their appearance. Considering that the stingless bees, unlike the social wasps, carry on the tradition of the solitary bees in feeding their young en masse rather than progressively, it is perhaps not inconsistent to expect that in regard to protandry, too, they would be more inclined

than the social wasps to abide by the ancestral pattern.

Finally there are two somewhat unusual instances, one of which is possibly due to an abnormal condition in the hive. Salt (1929, p. 439) mentioned that in a nest of *Trigona* (*Trigona*) *amalthaea* (Olivier) there were 26 royal cells, of which two contained adult virgin queens, two pupae, and the remainder larvae that had completed their growth. Yet a page later he added, "Males of this species were not obtained." Here would seem a case where protandry did not operate, although with commendable caution Salt does not affirm that males were absent but merely that they were not secured.

A nest of *Trigona* (*Trigona*) *compressa* Latreille, collected by W. Weyrauch on March 2, 1940, at La Merced, Peru, also presented a condition which at first sight is seemingly at variance with the conception of protandry. Nest material from this colony consisted almost wholly of males; of the specimens sent me 264 were males, only nine were workers. According to Weyrauch there was no evidence of royal cells, and even the royal mother could not be found.

The disproportion between males and workers, if constant throughout the colony, would indicate an unbalanced condition, with an incapacity of the queen to lay fertile eggs or even the absence of a physogastric queen. Weyrauch's failure to find such a queen may, therefore, be due to the fact that there was no queen to find.

The number of specimens, however, is inadequate for the formation of a final judgment. Possibly the males were more or less concentrated in a small area; possibly a fuller nest population would have revealed a much larger proportion of workers. I have even toyed with the idea that such a concentration of males may have foreshadowed the St. Bartholomew's Eve of extermination known as the slaughter of the drones. When the termite nest containing this colony of *compressa* was opened, there were also found in that termite nest five more or less inter-related communities of *Trigona* (*Trigona*) *chanchamayoënsis*, new species. All of these lacked royal cells and also virgin queens (in these respects resembling the nest of *compressa*), but all apparently lacked also

males, which is at variance with the nest of *compressa*. The date of observation of the two species (*compressa* and *chanchamayoensis*) is the same. May it not be that in the latter the slaughter of drones had only recently taken place while in the former the event was obviously still impending?

SLAUGHTER OF DRONES

The extermination of the drones is a familiar occurrence in the annual cycle of the honeybee. At the termination of the honey flow and when swarming has been completed, the drones are expelled from the hive. Contrary to popular belief they are usually not stung to death, but there is some evidence that before ejection from the hive they are deprived of food by the workers upon whom they depend for nutriment. Dragged out and henceforth barred admission to the hive, they die helpless outcasts from a community that no longer tolerates their presence.

What is the condition among the Meliponidae? Some of the earlier students of the group, Spinola (1842a, p. 218), for instance, drew the conclusion that, because these bees lacked a sting, a slaughter of drones was not feasible, but Spinola hardly gave adequate credit to their other means of destruction. In this family of bees, too, the time arrives when the male no longer is *persona grata*. An early reference presumably to the slaughter of the drones is contributed by Huber (1839, p. 22). His statement applied to *Melipona beecheii* Bennett and was based on observations made by the bee-keepers of Tempico, Mexico. It reads as follows: "At a certain season of the year they [the members of the hive] kill and cast out many bees, as those of Europe treat the drones; and the dead bees are the same size as the others."

In a hive of *Melipona fasciata* variety *rufiventris* Lepeletier that H. von Ihering (1903, pp. 203-204, 256) had under observation it was noticed that towards the end of March (in southern Brazil this would be about the beginning of fall) drones were forcibly removed from the community. The drones were seized by the wings and dragged to the flight hole. In one instance such a male was grasped by the left anterior wing by one bee and by the right anterior wing

by another bee. His adversaries would then start tugging, but he succeeded in freeing himself and escaping his tormentors. Another male, less fortunate, fell to earth close to the hive, along with the member of the colony that was carrying him. This male was in a semi-lifeless condition, presumably therefore it had been bitten. Such ejected drones, even if not wounded, were doomed to die outside, for, as in the case of *Apis*, the workers would bar their reentry into the nest. The slaughter of the drones, according to von Ihering, is not sudden or general. On the contrary, the elimination of the males stretches over days and possibly weeks.

Even in the case of the honeybee, drones are sometimes permitted to live on, but the reasons for this tolerance are not always clear. Perhaps such an exceptional condition obtained in the case of Rayment's stingless bees in Australia, prompting his statement (1932a, p. 186; 1935, p. 514) that, even after the fecundation of the young queen has been effected, the males are still permitted to enjoy the privileges of the hive.

Although the reported instances of an elimination of the drones are so few in the case of the stingless bees, there seems little reason to doubt that the phenomenon takes place. The paucity of the observations no doubt is traceable to the fact that so few living hives have been subjected to persistent and continuous study, with the result that an event that takes place only at intervals has frequently been overlooked.

VENTILATION

The ventilation of the nest through the rapid vibration of the wings, after the manner of the honeybee, has been noted in the case of various stingless bees. Drory (1872b, p. 190; 1873d, pp. 105-106), apparently the first to make this observation in the case of *Melipona fasciata* variety *scutellaris* Latreille, emphasized that the attempts at ventilation never took place outside at the nest entrance, always in the interior. In the case of *Trigona testaceicornis* variety *perilampoides* Cresson, too, ventilation seems to take place within the nest. At any rate, Michener (1946, p. 185) interpreted the steady humming sound that usually issued from nests of this variety whether by day or by night as indicative of

the fanning of wings. In contrast, the same observer noted that in the case of *Trigona* (*Trigona*) *fulviventris* Guérin "the nest entrance is lined during the day with many bees constantly fanning the air with their wings" (Michener, 1946, p. 190). This was the case also in a nest of *Trigona* (*Scaptotrigona*) *wheeleri* Cockerell that I observed at Cobán, Guatemala. Thus, it would seem that some species drive the fresh air inward from without while others force the stagnant air outward from within.

A section of a brood comb of *Trigona* (*Cephalotrigona*) *capitata* variety *zexmeniae* Cockerell was placed by Salt (1929, p. 442) in a closed box over night. On the following morning when Salt inspected the comb the bees were on the cells actively fanning to the accompaniment of a steady buzzing. Salt noted that "this fanning produced a decided cooling effect, pleasant to feel with the hand."

Yet another observer, Rayment, noted (1932a, p. 186; 1935, p. 513) that the stingless bees regulate the temperature of the nest by a fanning action of the wings. His studies were based on Australian species of *Trigona*.

COMMUNAL FLIGHT ACTIVITIES

Several observers have noted large, rather compact flight groups of stingless bees engaging in aerial maneuvers, usually rather close to the nest. Such a flight was observed by Schulz (1905c, p. 143) in the case of the New World *Trigona goeldiana* Friese, commonly regarded as a synonym of *Trigona minima* Gribodo. It took place in the hot midday hours and resembled a dance of midges. As midges, Horne (1870, p. 185) had similarly interpreted the Indo-Malayan insects that in a swarm consisting of from 400 to 500 individuals were "rapidly flying about in a mazy kind of dance, occupying a space of five or six feet, and being about ten feet from the ground." Only when the insects were caught was the fact revealed that, instead of midges, the flight participants were *Trigona* of the species *ruficornis* F. Smith, later (C. T. Bingham, 1897, p. 563) redesignated *smihii*.

Salt (1929, pp. 442-443), who gave an interesting account of certain flight exercises of a large number of *Trigona* (*Tetragona*) *nigra* variety *paupera* (Provancher) is careful

to note that the participating bees, unlike crane flies and midges, engaged in no wave motion or levitation up and down. "There was simply the speedy dash of the insect from one side of the aerial course to the other, a twist, a turn or a sudden stop, and back again to the other side," all executed within an aerial space about 6 feet square. The same observer (1929, p. 444) noted a flight of similar character in the case of *Trigona* (*Nannotrigona*) *testaceicornis* variety *tristella* Cockerell. The flights of both species took place in the morning and in each instance all of the many specimens examined were workers. Similarly all the specimens Schulz collected from the *goeldiana* aggregation referred to above were workers.

It is possible, of course, that the flights observed by Salt were of a different character from those reported by Horne and by Schulz, especially as Salt disassociates the phenomena he observed from the aerial dances of midges, while both of the other authors specifically draw comparison with such manifestations. On the other hand, the fact that *paupera* as observed by Salt indulged, as did the aggregations of bees noted by the other two authors, in flight exercises mostly near the nest makes me think that, whatever may have been the significance of the performances, a common purpose probably underlay all of them.

In the dance of *paupera* observed by Salt callow individuals predominated, and because of this Salt was inclined to interpret the flight "as concerned with the maturation of young workers." Neither Horne nor Schulz indicated whether callow individuals were represented in these flight demonstrations, but specimens of *Trigona* (*Tetragona*) *fuscobalteata* Cameron (all workers), collected by H. T. Pagden on February 24, 1928, at Kuala Lumpur, Malaya, were in a "swarm" and included individuals showing various degrees of maturation from callow to adult coloration (Schwarz, 1939c, p. 107). This leads me to believe that the "swarm" was a flying aggregation of bees resembling the other flight assemblages described, and because of the participation of callow specimens I find it tempting to adopt Salt's explanation. At least no better explanation suggests itself.

The observations made by Salt on *paupera*

were supplemented by observations made on the same species and variety by E. McC. Callan at Talparo, Trinidad, British West Indies, April 4, 1943. According to R. G. Donald, who transmitted some of the specimens to me: "These bees were seen swarming around a house and a few sweeps with a net secured 159 specimens. Of these 108 had a white abdomen, 40 had a white abdomen with distinct dark bars, and 11 had the abdomen uniformly black. Dr. Callan reports that the insects flew exceedingly rapidly, darting back and forth so quickly that they gave the appearance of a network of fine white lines."

Brunet in the seventies of the last century made observations on domesticated hives he had installed in Bahia, Brazil. He hesitated to express an opinion whether new nests are established by swarms or not, having never witnessed the phenomenon. However, he went on to say that he had often been tricked into believing that his stingless bees were swarming because of large assemblages resembling "a thick cloud" which they formed a short distance from the hive, but "after these evolutions" the putative swarm always reentered the nest. Here, it would seem, we again have an instance of the type of phenomenon presented. The species of bees participating in each demonstration are not mentioned, but, as Brunet stated that he had "often" seen these happenings, it is perhaps fair to assume that certainly more than one species was involved in the successive demonstrations (cited by Raveret-Wattel, 1875, p. 752).

It may be that Wheeler's reference (1913, p. 2) to an incipient act of swarming on the part of *Trigona* (*Trigona*) *amalthaea* (Olivier) belongs also to the category of happenings here discussed. At any rate, "the air about the nest was full of bees flying back and forth in zig-zag paths like those described by some dancing Empidid flies." But there was this additional development not observed on the other occasions: "A compact mass of the insects had settled to one side of the entrance spout." When Wheeler put his tweezers into this mass, he was "at once enveloped in a cloud of humming bees," which, contrary to the usual behavior of these insects, darted at him without alighting and fre-

quently fell to earth or on his clothing. "They moved very rapidly and as if intoxicated," wrote Wheeler, and it was probably this rather unrestrained excitement that prompted Wheeler to interpret the act as one connected with swarming, for the behavior of the honeybee during swarming is sometimes spoken of as comparable to intoxication, "swarm dizziness" and "bacchanal delight" being terms that have been employed to describe the delirious behavior of *Apis* on such occasions.

It has been noted that in the flight assemblages recorded by Salt and by Schulz the specimens secured were all workers. However, males, too, participate in flight assemblages and in such cases can be equally exclusive. Before me is a series of stingless bees received from Mr. Alfonso Dampf. They bear his field number (FM2780) and were secured in Frontera Hidalgo, Mexico, on the border of Guatemala, at four o'clock in the afternoon of September 18, 1932, "swarming in air." Thirty-four specimens were sent me and all of them are males of the subgenus *Scaptotrigona* but, while 32 of them are assignable to *luteipennis* Friese, the remaining two belong to the rather different *pectoralis* Dalla Torre. Bequaert stated (1932, p. 17) that many males of *Trigona* (*Cephalotrigona*) *capitata* variety *zexmeniae* Cockerell were observed on the leaves of bushes near the entrance to their nest or hovering in its vicinity.

Thus we have spinster gatherings and bachelor gatherings in the communities of the stingless bees.

An interesting observation regarding the congregating of males was made at Panama City, Canal Zone, by C. D. Michener. The species involved was *Trigona* (*Tetragona*) *jaty* F. Smith.

"For the last two days," wrote Michener, under date of January 5, 1945, "an estimated 500 male *Trigona* were seen swarming around the entrance of the nest. Part of the time they were all in the air, flying in a swarm about three feet in diameter, while at other times most of them gathered a few feet from the nest in two or three dense groups covering several square inches on the wall of the building.

"Each time these males were disturbed

they quickly disappeared, dispersing into the open, but they soon returned to swarm or gather in groups again."

An aggregate of 91 of these males was subsequently sent me.

The nest to which these males belonged was unfortunately destroyed shortly thereafter by someone who was more annoyed by the presence of the insects than curious to study and know their ways. At any rate, Michener's opportunity to continue the investigation was cut short by this untoward action. Nevertheless, he had a chance to note that even after the destruction of the nest the bees manifested similar behavior to that above described for about a day.

He made an examination of a part of the injured nest and took from it no fewer than 196 individuals. All of these proved to be workers, a fact in itself interesting in view of the large flight aggregates of males both in the period before and after the mutilation of the hive.

On February 16, 1945, he noted a further swarm of *jaty* near the entrance to a nest that was in a small cavity at the base of a large tree at Pacora, Panama. Bees from this aggregate to the number of 267 he kindly sent me. The overwhelming majority, 259 of them, somewhat to my surprise turned out to be workers, but eight males had in some way become members of the group.

Michener continued his studies of *jaty* and by April 15, 1945, when he again wrote me, he had located no fewer than 29 nests of this species in Old Panama, Panama.

"Males swarm in front of the nests frequently," stated Michener, "sometimes in immense numbers, often in small numbers. I have noted swarms at all times of the day and throughout the period that I have been in Panama [December, 1944, to April, 1945]. Unlike the swarms of other species studied, those of *T. jaty* quickly disperse, if disturbed, but reassemble in a few minutes. While a few workers are often present in collections made from swarms, it is probable that these are specimens caught as they were flying to or from the nest." Later (1946, p. 188) Michener offered as the more probable explanation the surmise that the small number of included workers was recruited from the one to eight or 10 members of this caste commonly found

dancing within a few inches of the nest entrance.

The same observer noted other aggregations of bees. Males were observed before two nests of *Trigona* (*Trigona*) *fulviventr* variety *fulviventr* Guérin. These assemblages consisted of only 25 to 50 individuals and "of these only about half were flying about at any one time. The remainder were scattered about, resting on leaves, twigs, and tree trunks within 18 inches of the nest entrance" (Michener, 1946, p. 190).

The observations on *fulviventr* were made in May and in July. Later in the year (August 5, 1945) Michener had a chance to note an aggregate of males of yet another species, *Trigona* (*Scaura*) *latitarsis* Friese, which in large numbers were swarming around a nest within an arboreal termite colony. The observation was made at Cerro Campana, Panama (Michener, 1946, p. 195).

In the case of *Trigona* (*Nannotrigona*) *testaceicornis* variety *perilampoides* Cresson males were "seen swarming in front of nests at all times of day, and at all seasons of the year" (Michener, 1946, p. 186).

Assemblages of males are not confined to *Trigona*. On March 25, 1945, at 2 P.M., Michener noted a group of about 25 males, apparently far from any nest opening. The species proved to be *Melipona favosa* variety *phenax* Cockerell. "Some of them," wrote Michener in a letter to me, "were buzzing around but most were resting in a small crevice out of the wind but in the sun. Five other nests showed no such activity at that time. On March 27 at 9:45 A.M. the same phenomenon was observed, this time with some 35 individuals." Another aggregate observed consisted of as many as 70 individuals. "At no time," stated Michener (1946, p. 184), "was a nest opening discovered close to such a group."

Even the absence or rarity of such assemblages in certain species has its interest when compared to the abundant evidence that in other species they occur with frequency. Thus Michener (1946, p. 193) commented to the effect: "I have not seen males swarming in front of the nests of this species [an undescribed variety of *Trigona* (*Paratamona*) *testacea*] and suspect that they may not do so. On April 9, at 11 A.M., several

males were found resting on the rocks within about six inches of a nest. When disturbed they buzzed about but did not attack as the workers do."

As Michener had under observation as many as 44 nests of this bee (36 of them in the walls of Old Panama) his failure to note any significant assemblage of males is indicative that at the season, at least, during which he made his observations such occurrences are a rarity or simply do not happen. On the other hand, there are before me two fairly large series of this variety consisting entirely of males in one case and almost exclusively of males in the other case and, until the receipt of Michener's report, I was inclined to think that they were probably such a bachelor assemblage outside of the nest as has here been described. One of the series in question was collected by Mr. T. Hallinan at Farfan, Panama, February 28, 1915, and the second series by Dr. A. Alfaro at San Isidro, Costa Rica, August 7, 1937.

One is puzzled to find a meaning for these assemblages. Mention has been made of the suggestion offered by Salt that in the case of the workers, at least, these communal activities are flights of maturation. But a similar explanation does not apply to the males, which are mature individuals and in some of the instances cited are resting rather than active. Could it be that they are expelled members of the hive, no longer wanted by the Amazons of the colony? The absence of any males among the individuals rescued by Michener from the destroyed colony of *jaty*, when only a little before that catastrophe an estimated number of 500 of this sex had been swarming around the nest entrance, may suggest such a conclusion. On the other hand, the activity displayed by some of the groups of males and the fact that they are un mutilated and bear no marks of injury hardly point to a forcible ejection from the nest. Another possible thought is that the males are awaiting the emergence of one or several of the princesses of the nest, but this surmise is subject to the challenge that, were this the case, surely an act of mating or at least a pursuit of an emerging member of the royal caste would ere this have been noted. Perhaps it is just a case of birds of a feather flocking together, but when one

draws on the imagery of ornithology to try to explain the ways of the bees, one may well be farther from the truth than ever, and so the finding of a convincing explanation must be left to future observation and study.

SWARMING

Writing in 1836 (p. 415) Lepeletier listed among the many things regarding stingless bees of which the world was then ignorant: whether or not they multiplied their colonies by swarming. An affirmative answer to this question was given 32 years later by Peckolt (cited by F. Smith, 1868, pp. 133-134), who saw *Trigona (Trigona) ruficrus* (Latreille) swarm. "A great number left their hive, with their queen," stated Peckolt, "just as I have seen the honey-bee, *Apis mellifica*, and indeed their mode of life appears to be almost identical."

If Peckolt's concluding statement just quoted carries with it the implication that the old queen rather than one of her daughters participates in the flight of the swarm, this deduction fails to find support among such students of the stingless bees as Drory (1877, p. 146), Hockings (1884, p. 154), Silvestri (1902b, p. 166), H. von Ihering (1903, p. 181), Berlese (1925, p. 824), Bouvier (1921, p. 211; 1926, p. 159), von Buttel-Reepen (1903b, p. 54), Wheeler (1928, p. 101), and Weber (1933, p. 598; 1938, p. 203). It is far from clear, however, whether or not these later conclusions, which deprive the old queen of the role of founding the new colony, are based on observation. More likely the belief is governed by the fact that the old queen, sluggish and obese and dragging herself about the hive with a preponderantly heavy load of eggs in her abdomen, is so poorly equipped for flight that it seems out of the question that her wings could sustain the weight of her body. The virgin queen, it is true, has wings of identical character with those of the old queen (except that those of the old queen are usually frayed) but her body weight, owing to the absence of eggs, is much easier to lift.

Peckolt, who communicated his observations to F. Smith in the late sixties of the last century, recorded his impressions of swarming in greater fullness in the nineties. It is to the swarming of *Trigona (Trigona) ruficrus*

(Latreille) that he particularly devoted the account (Peckolt, 1894, p. 224). A colony of *ruficrus* had found lodgment on March 8, 1866, following a storm, in a box that Peckolt had intended for the accommodation of some pigeons. Near by was a similar box which had actually been occupied for a time by pigeons but was subsequently deserted by these birds. On March 3, 1867 (the date is worth noting, for it is almost exactly a year from the time when the swarm just mentioned had taken possession of the box that we shall designate No. 1), there occurred in the afternoon at two o'clock a storm. "When the storm broke, there was," stated Peckolt, "a great commotion accompanied by strong humming. Outside of the box [No. 1] were a large number of bees, as well as a few specimens in the neighboring empty dove box [No. 2]. After a quarter of an hour there began a flight in numbers into this box [No. 2] and, outside and within, this box swarmed with bees. By 5 P.M. no bee was present on the outside of the box and complete silence reigned. By next morning great activity was already noticeable. The bees worked with incessant eagerness on their new dwelling." On March 8 of the following year (1868) again there was a storm and again there was a swarming. Peckolt unfortunately was not on hand and he could not determine, therefore, which of the two colonies housed in the neighboring boxes had given forth the swarm or whether indeed both had contributed to the new colony. It is worth emphasizing that again the date of swarming is March and the day of the month is the very same as that on which the first act of swarming was observed two years before.

Peckolt's observations on the swarming of *ruficrus* are of great interest. To be noted is that each of the three acts of swarming took place during a thunderstorm. The honeybee, on the other hand, usually selects a clear bright day on which to set forth on this significant adventure (Phillips, 1928, p. 72). Even more deserving of emphasis is the season of the year during which the several acts of swarming took place. At Cantagallo, in southern Brazil, where Peckolt made his observations, March, or at least the end of March, marks the beginning of the cold season (*in* F. Smith, 1868, pp. 133-134).

Planters of the region assured Peckolt that *ruficrus* swarmed twice a year, in August as well as in March. If this should be the case, the August date would accord with, or more nearly approximate, what is the usual season of swarming in the case of certain other *Trigona* observed by Peckolt. Thus he noted what he interpreted somewhat doubtfully as a swarm of *Trigona* (*Plebeia*) *mosquito* F. Smith taking its flight at the opposite extreme of the year from that noted in the case of his populations of *ruficrus*, namely, in September. Summer would seem the opportune time for starting a new colony, and September, the beginning of summer in southern Brazil, is the month of the year in which Peckolt (1894, p. 89) observed in the act of swarming not only *mosquito* but also a larger bee, which, probably incorrectly, he designated *Trigona* (*Tetragona*) *jaty* F. Smith. In September, too, he noted the swarming of yet another stingless bee, which he interpreted as *Trigona* (*Scaptotrigona*) *bipunctata* (Lepeletier), and this same species had been observed by him swarming as early as late August of a previous year.

George (1934, p. 5) stated that at Coimbatore, India, swarms are given off by the older hives usually in August or September. In the same paper (p. 3) he indicated that the honey season is from March to June, the true summer, which is also the season of prolific breeding in the case of the species to which he gave special study, namely, *Trigona* (*Tetragona*) *iridipennis* F. Smith. The mild winter in the region falls in the months of December, January, and February. Thus the season of observed swarming would in this case seem to fall about midway between summer and winter. Another observer in India, Castets (1893, p. 485), expressed the opinion with respect to *iridipennis* that it probably swarmed "every two months whereas other bees, even in the plains, swarmed only two or three times a year." The basis for this assertion is not clear.

According to field records supplied to Rayment (1939, p. 293) a "swarm" of *Trigona carbonaria* F. Smith was observed "issuing from a cavity in a tree as a thick, fast-moving 'ropy' spiral, having a diameter of eight inches."

Mention has been made of the readiness

with which a swarm of *Trigona* (*Trigona*) *ruficrus* (Latreille) took possession of a neighboring empty box for the purpose of establishing its new home. Similarly H. von Ihering (1903, p. 256; also cited by Sapper, 1935, p. 184) told of a swarm of *Melipona quadrifasciata* variety *anthidioides* Lepeletier that occupied an empty chest conveniently near the parental nest and presently replaced the missing lid by a batumen plate measuring fully 10 cm. in thickness. Thus it would seem possible to capture a daughter swarm of stingless bees as readily as an escaping swarm of honeybees provided the proper housing facilities are offered at the time when the swarm is emerging.

What occurs in situations that are controlled by man repeats itself under more or less identical conditions in nature. If suitable living quarters are available near by, there is little temptation to seek for the same thing afar. Where two or more colonies of the same species of stingless bees occupy the same tree or adjacent trees, the inference seems justified that one of the colonies is the parent colony and the others are daughter colonies. Four such colonies, all in a single tree, were reported by H. von Ihering (1903, p. 215) in the case of a stingless bee close to *Trigona* (*Scaptotrigona*) *postica* Latreille. Five nests belonging to a bee of the subgenus *Partamona* were found by Rau (1933, p. 18), all located on one of those leafless dead trees that lift their barkless trunks and barren branches high above the water close to Barro Colorado Island, Canal Zone, ghostly survivors of the tree growth that covered areas now submerged, before the construction of the Panama Canal. Two nests of *Trigona erythra* variety *togoensis* were reported by Stadelmann (1895, pp. 618-620) as occupying the same tree hollow in immediate proximity to each other.

Dreher counted in a single tree no fewer than seven nests, each separated from the other by a batumen plate and functioning as a distinct colony (H. von Ihering, 1912, p. 43). Presumably all of these seven nests were nests of *Trigona* (*Scaptotrigona*) *postica* Latreille (identification of Friese) or of *Trigona* (*Scaptotrigona*) *bipunctata* Lepeletier (identification of Schrottky). The presence of several colonies of the same species within

a single tree suggests the likelihood of a parent colony and daughter colonies, but it is probable that, even in such cases, the impelling motive for settlement is a conveniently available nest site that meets the standards of the bees rather than any feeling of neighborliness. Elsewhere (p. 12) mention was made of a tree holding 25 nests. One cannot resist wondering how many of them may have been nests of a single species.

Most of the instances reported of the close proximity of nests of the same species are concerned with arboreal nests, or with nests in the walls of buildings, as in Old Panama (see p. 12). Yet Peckolt (1894, p. 90) was inclined to believe that daughter swarms of ground nesting species might similarly build their new establishments close to the parental home. Only thus was he able to interpret four spherical masses that he believed to be independent nests, all found in the course of excavating the nest site of *Trigona* (*Schwarziana*) *quadripunctata* variety *bipartita* (Lepeletier).

Very likely Peckolt is right. The problem is somewhat comparable to that presented by a discovery of Weyrauch, who in the case of *Trigona* (*Trigona*) *chanchamayoensis*, new species, established in a termite nest at La Merced, Peru, found no fewer than five brood chambers (only two of which had supplementation of provision jars). All five were reached by passageways leading inward from a common entrance tube. Here possibly was a case of rather incompletely individualized daughter nests. Only a single physogastric queen was present, with the implication that she may have been the mother of all the several populations. (See p. 310.)

Not always are contiguous nests occupied by members of the same species. Alien groups may also live in close association. The five associated communities of *chanchamayoensis* referred to in the previous paragraph shared the not too spacious termite structure with yet another species, *Trigona* (*Trigona*) *compressa* Latreille, that had likewise established itself there. No fewer than three different species of stingless bees were noted by Salt (1929, p. 435) occupying nests in the hollow trunk of the same tree. They were: *Melipona interrupta* variety *salti* Schwarz and, farther down the trunk, *Trigona* (*Trigona*) *amalihea*

(Olivier) and *Trigona* (*Cephalotrigona*) *capitata* variety *zexmeniae* Cockerell. Furthermore Mr. Vincent Baker sent me recently five different species of stingless bees, all collected from a single tree 20 km. south of San Felix on the Orinoco River, in the State of Bolivar, Venezuela. Three of these species had their nest within the "creviced and tunneled interior" of the tree; the other two species were apparently intruders. According to Mr. Baker's memory, the permanent residents of the tree were the species I identified for him as *Melipona favosa* variety *favosa* (Fabricius), *Trigona* (*Cephalotrigona*) *capitata* variety *capitata* F. Smith, and a species of the subgenus *Scaptotrigona*. The intruders were seemingly *Lestrimelitta limão* (F. Smith), a species well known for its depredations, and *Trigona* (*Trigona*) *hyalinata* variety *branneri* Cockerell. But the interesting fact, irrespective of the particular species involved, is that three of them shared the same tree as a nesting site.

The establishment of daughter colonies from a parental hive seems a natural development. More unusual would appear to be the complete desertion of the parental nest by all of the inmates. True, *Apis dorsata* is said to indulge in such mass migrations to another nest site and it is not inconceivable, therefore, that other social bees might on occasion behave similarly. Goudot (1846, p. 713; cited by Gronen, 1881b, p. 333) recorded that in Colombia he was told by the natives that domesticated colonies of a member of the subgenus *Tetragona* would sometimes set forth after a time from the nest assigned to them in order to seek the wide spaces, both the old generation and the new joining in the migration. But this reported happening needs confirmation. At least the physogastric queen, because of her inordinate weight and inade-

quate wings, would seem incapable of participating in such an exodus.

FLIGHT OF ORIENTATION

A colony of what seems to have been *Trigona* (*Tetragona*) *iridipennis* F. Smith was under observation by Jacobson in Java before being shipped to Schulz (1909, pp. 338-341) in Germany. Jacobson noted that most of the bees before leaving the observation box in Jacobson's home, to which the colony had been temporarily transferred, circled about the nest entrance with their heads directed towards the hive just as the honeybee does under similar circumstances (cited by Friese, 1914a, p. 55). A like observation is reported by Rayment (1932a, pp. 246, 250; 1935, pp. 530, 533) in the case of colonies of the Australian *Trigona carbonaria* F. Smith and *Trigona cassiae* Cockerell, which were given access to the outer world after a period of incarceration while in transit to Sandringham, Victoria. H. von Buttel-Reepen (1907, p. 467) alluded to a flight of orientation in front of the nest on the part of *Trigona* (*Plebeia*) *mosquito* variety *emerina* Friese.

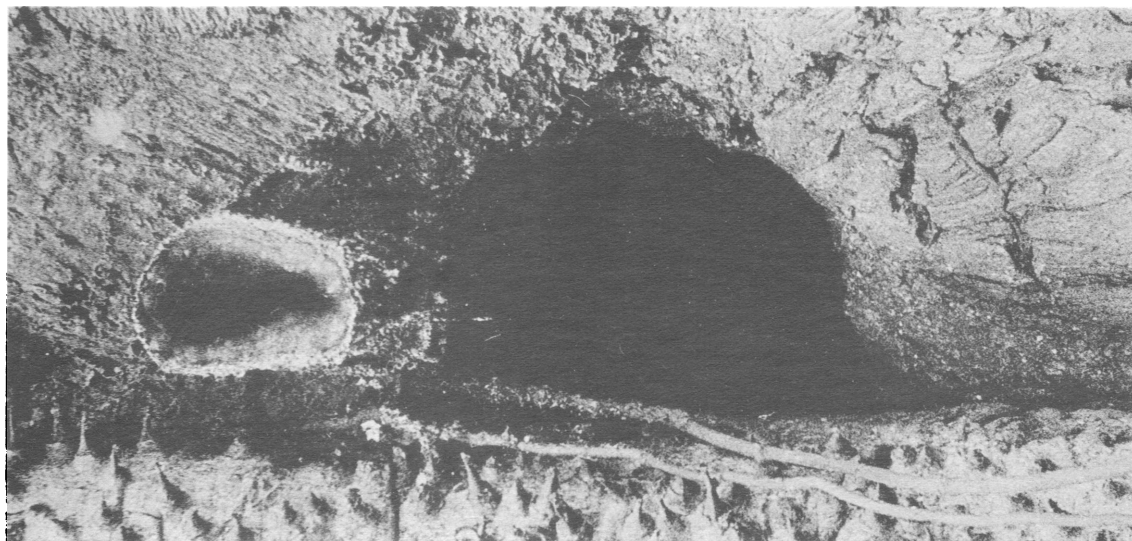
Some observers have claimed that stingless bees master the location of their nest more rapidly than does the honeybee. This has been stated more particularly with reference to *Melipona fasciata* variety *scutellaris* Latreille. Thus it is the contention of Girard (1875a, p. 571) that, if a hive of honeybees be shifted about, each departing bee makes several gyrations about the nest entrance, whereas *scutellaris* under similar circumstances seems to gain the requisite knowledge of the new environment with a single circuit of the entrance. Layens, who had supervision of the hive of *scutellaris* at an exhibition of stingless bees in Paris in 1874, placed the hive nearly every morning in a different position

PLATE 1

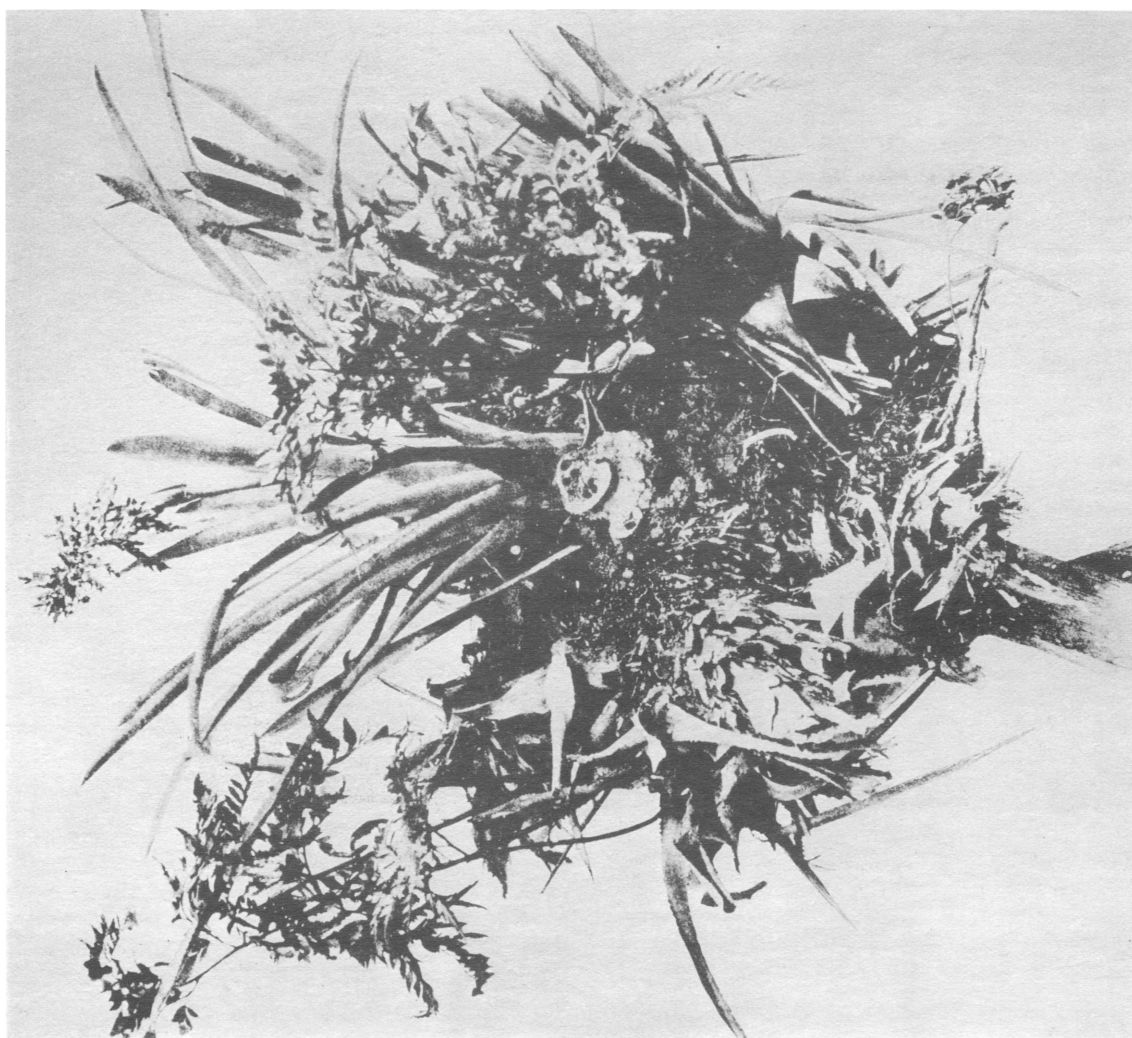
1. Nest of *Trigona* (*Partamona*) *testacea* variety *helleri* Friese built between bromeliads. After H. von Ihering, based on a specimen in the Museu Paulista. This is a nest site sometimes adopted by species that ordinarily build in the hollows of trees or elsewhere.

2. Flight tube of *Trigona* (*Trigona*) *fulviventris* Guérin. The nest was located in a sandbox tree (the "Allee tree") on Barro Colorado Island, Canal

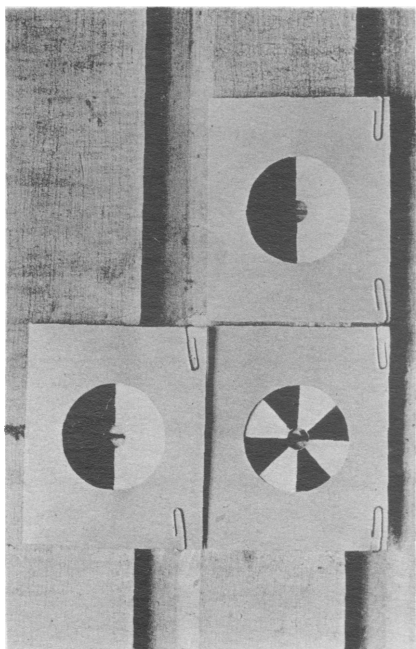
Zone, and a replica of it has been installed as an exhibit in the American Museum. Ordinarily large flight tubes like that of *fulviventris* are guarded by row upon row of bees lined up within the tube and facing outward, and this was usually the case also in this very tube. At the close of day the bees retreated inward into the nest, and by about 6 P.M. withdrawal into the interior was nearly completed. From a photograph by Frank E. Lutz.



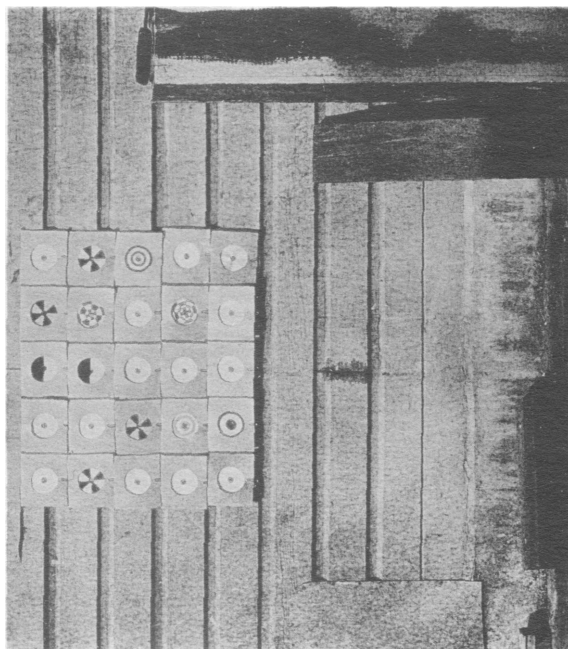
2



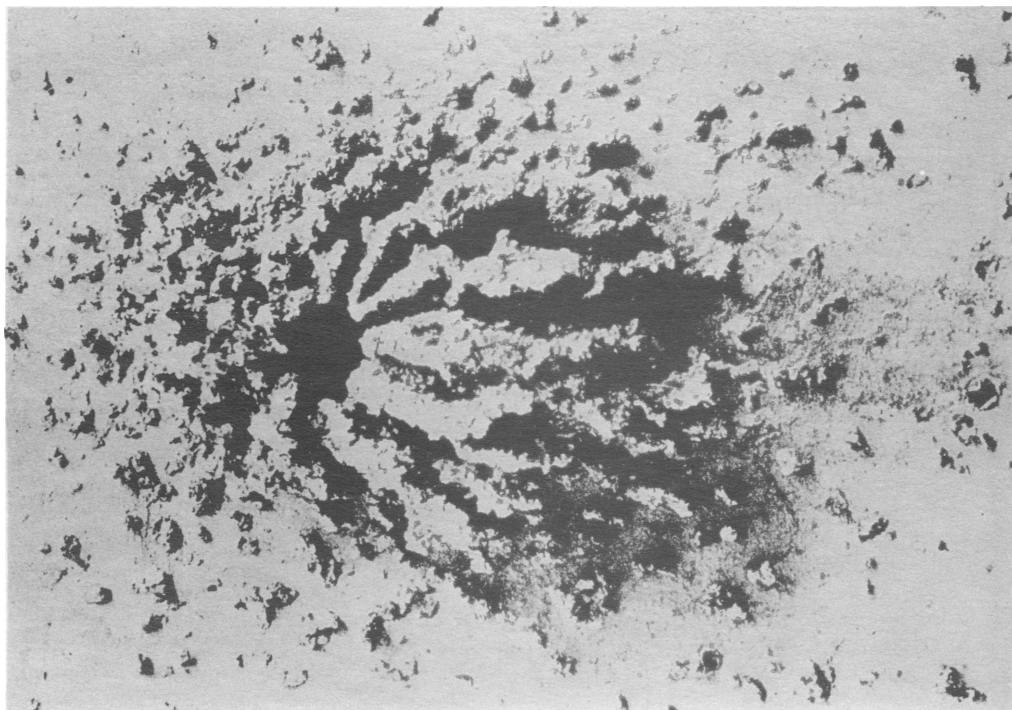
1



2



3



1

and observed the speed with which the bees departed from the nest after a minimum of orientation (cited by Raveret-Wattel, 1875, p. 748). In observing a nest of *Trigona* (*Tetragona*) *nigra* variety *paupera* (Provancher) on Barro Colorado Island, Canal Zone, I noted that sometimes individuals of the nest darted out without a preliminary flight of orientation, but as there were every so often among the bees that returned to the hive some that were unladen, I was inclined to believe that these burdenless bees were possibly the same as those that had left the nest so unceremoniously for what may have been merely impulsive and very localized flight

efforts in distinction to the wide ranging of the fields by the pollen gatherers.

The flight of orientation is a preliminary to departure for distant excursions, especially foraging expeditions that take the individual bee far from the home community. It has seemed best to reserve for a later section an account of foraging and materials foraged because, while these activities are of benefit to the colony, they are carried on in the world at large rather than at home. But something should be said at this point regarding the different classes of citizens that constitute the insect state we have just been considering.

THE DIFFERENT CASTES AND GROWTH STAGES

WORKER

Except for her limitation of egg laying the meliponid worker has retained within her scope of activity the functions, such as nest construction, pollen and nectar gathering, and the like, which in the case of the solitary bees are performed by the female. With these

functions are associated the anatomical structures that make these functions possible of achievement. The worker is, therefore, far more representative of her species than is the degenerate queen.

Owing to the fact that the worker is the individual above all others whose daily round

PLATE 2

1. Exterior of nest of *Melipona quadrifasciata* variety *anthidioides* Lepeletier. The flight hole giving admission to the interior of the nest is represented by the dark, irregularly circular area near the center, from which radiate the ridges of earthen material. The photograph, taken by José Marianno, is based on a domesticated colony.

2, 3. Cards used in the experiment performed by Frank E. Lutz on Barro Colorado Island, Canal Zone. A colony of *Trigona* (*Tetragona*) *nigra* variety *paupera* (Provancher) had built a nest within the wooden wall of one of the buildings of the Institute for Research in Tropical America. Lutz tested the ability of these bees to recognize different geometric designs placed over and about their nest entrance as well as their ability to differentiate between white color that reflected ultraviolet and white color that did not. Some of the constituent cards in 2, and more particularly in 3, seemed of identical color as well as of identical pattern to the human eye but, because of the different quality of the white paint used in each, they were essentially different. The eye of the bee, the experiment proved, could detect this difference even though the human eye could not. In the experiment one card was placed over the flight hole,

which in this species lacks an external flight tube. After the bees had accustomed themselves to associate that card with the portal of the nest and had repeatedly entered the nest through the hole provided in the center of the card, other cards were gradually added until finally a total of 25 cards were arranged in the completed rectangle of cards. During all this time the bees were not diverted by the additions. They remained faithful to the design that gave admission to the nest. This fidelity was based on recognition of pattern and color rather than of relative position, for the cards other than the one covering the nest entrance were frequently shifted without confusing the bees. Then the final step in the experiment was taken. A fresh card, identical in all respects as to pattern and sequence of colors with the card that covered the nest entrance, was prepared so as to preclude the possibility of there being an association of nest odor with the card, and this new card (the twin of the significant card that had been removed) was added to the card mosaic but *in a new position*. The bees still recognized it notwithstanding the dislocation and continued to come to this card by preference instead of to the other cards. From photographs by Frank E. Lutz.

of duty takes her far afield from the nest, it is the worker that is most often collected. Even when specimens are obtained from the flight hole of the nest, again it is the guarding workers that will figure in the captures to the exclusion usually of the other castes, and it is as a rule only when a deeper penetration of the nest is attempted that the males and queens are obtained.

Because so much of the essential work of the hive devolves upon the worker, much of the account given in this Introduction is devoted either directly or indirectly to her activities. Her structure generally indicates her fitness for the task involved. Her eyes are larger than those of the queen, whose life, once egg laying has begun, is destined to be spent in the darkness of the hive where the compound eyes are probably of only limited service. The head of the worker is at least relatively wider than that of the queen. She shares with the queen, however, the twelve-jointed antennae so characteristic of the female throughout the Apoidea that, when a larger number of joints occurs (as in what Cockerell described as the genus *Androgynella*), suspicion has subsequently been voiced that the aberrant individuals were gynandromorphs of a species normally having 12 joints in the female antennae. The mandibular structure is often highly specialized in the worker and frequently is a character on which, along with other characters, reliance can be placed in establishing subgeneric distinctions. Notable for the characteristic structure of their mandibles are the workers of the subgenera *Trigona* and *Paratrigona* (both completely toothed along the apex), *Cephalotrigona* (with a large tooth at the inner extremity of the apex), and *Scaura* (edentate along the apex).

It is in the structure of the hind leg, where not only are deposited loads of pollen but also the building materials needed for the construction of the nest, that the greatest specialization of structure occurs. Here is the corbicula, or pollen basket, a depressed or flattened area towards the apex of the outer face of the tibia but in some subgenera of *Trigona* extended upward over a considerable part of the joint. Along the anterior lateral margin as well as along the posterior lateral margin are fringes of hairs that assist

in holding the load captive. The hairs of the posterior fringe in some subgenera (*Trigona* and *Tetragona*) are plumose, thus more effectually functioning in the retention of the burden. On the outer face of the tibiae and placed anteriorly at their apex is a compact comb of curvilinear spines springing from a more or less common base. The comb juts out somewhat from the joint and, while feebly developed in some of the species of minute size, is characteristic of the worker throughout the genera *Melipona* and *Trigona*. It is supplemented in these genera by a comb-like row of spines or spine-like hairs inward along the apical margin of the hind tibiae. Both the anterior comb and the row of spines are lacking in the genus *Lestrimelitta*, and the anterior comb at least is confined to the worker caste in *Melipona* and *Trigona*.

The abdomen has six visible segments in addition to the propodeum. It is the quarry from which essential building blocks in nest construction are derived (see section on wax production, pp. 43-44).

Great difference of size may occur between the individuals of one species and those of another species within the Meliponidae. Such contrasts are particularly striking in the case of the worker (pl. 6, fig. 2) and also of the male.

QUEEN

Frederick Smith (1866, pp. 324-326) described what he believed to be the first member of the royal caste of *Trigona* to be recorded, but Erichson a quarter of a century earlier (1841, p. 219), as well as Klug (1843, pp. 219-221), very definitely had recognized queens of this family, and Spinola (1842b, p. 267) dissected a queen of *Melipona beecheii* variety *fulvipes* Guérin. Spinola's dissection was made fully 30 years before Drory (1872b, p. 206) sent von Siebold a queen of *Melipona fasciata* variety *scutellaris* Latreille under the mistaken impression that never before had a *Melipona* queen been studied anatomically. Smith's description of the queen of *Trigona* (*Plebeia*) *mosquito* nevertheless is the first moderately detailed description to be given of that caste in a given species of Meliponidae. It was soon followed by a description of the virgin queen of a *Melipona*, namely, *scutellaris*, by Drory (1872b, p. 159).

Melipona queens emerge from cells no larger than those of the worker or male; *Trigona*, on the other hand, have distinct royal cells at least in those species that build their brood cells in combs and probably also in most or all species that arrange their brood cells in clusters. The physogastric queen is readily recognized in both *Melipona* and *Trigona* by her distended abdomen, but the virgin queen of *Melipona* at least is no larger, if anything a little smaller, than the co-specific worker. In contrast, the *Trigona* queen has a thorax that is impressively larger than that of the worker or the male, and this, as well as her robust legs, gives her even in the virgin state a stature that readily sets her apart from the other members of the colony. What has been said of the queen of *Trigona* applies also to the queen of *Lestrimelitta*.

The stingless bee queen shows in her structure the degeneration concomitant with the relinquishment of many of the functions performed by solitary female bees and in the Meliponidae taken over by the worker. Her head is either actually smaller (*Melipona*) or at least relatively smaller (*Trigona* and *Lestrimelitta*) than that of the conspecific worker, failing in both cases to extend in width for a space equal to that measured from the outer edge of one of the tegulae to the outer edge of the other tegula. The eyes are reduced in size when compared to those of the worker and still more notably so when compared to those of the male. Where the mandible shows characteristic armature in the worker, this armature is often enfeebled or degenerate in the queen. The malar space is always distinctly longer than that in the other two castes. As in the worker but not the male, each antenna consists of 12 joints.

The hind legs of stingless bee queens, no longer dedicated to the task of carrying pollen or building material, are not specialized for these functions, although in some forms the lateral fringing hairs are strongly developed. The hind metatarsus tends to be wider at the base than at the apex (sometimes, as in *pallida* and *chanchamayoensis*, it is of rather uniform width) and approximates in length the combined length of the lesser tarsal joints. It is narrower than the hind tibia even in the subgenus *Scaura*,

of which the worker and the male have swollen hind metatarsi.

The wings are at least relatively and often actually shorter than those of the worker and male, and are frequently so frayed that they are still further reduced to impotence. They show other evidences of degeneration, too (see the section on a comparative study of the hamuli in the social bees, p. 119).

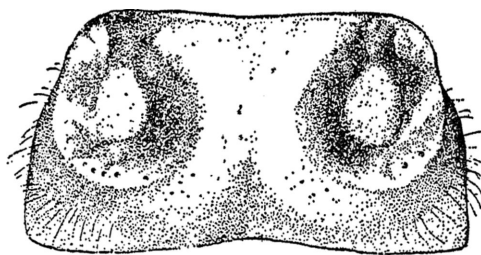


FIG. 2. Basal abdominal tergite of queen of *Melipona flavipennis* F. Smith, showing the circular depressions at each extremity, with a channel-like outlet at the upper end, that is found in the royal caste of some stingless bees. Drawing by Edna L. Beutenmüller.

The bloated abdomen of the physogastric queen bears little resemblance to the much shorter, more mobile, telescoped abdomen of the worker. In some forms (more particularly in *Melipona*) the virgin queen has a circular depression on each side of tergite 1, with a channel-like outlet at the upper end (fig. 2). Each of these depressions, when present, occupies about one-third of the width of the tergite and the basal half of its length. The last visible sternite (sternite 6) is sometimes more or less characteristically shaped.

The queen is often more abundantly hairy than is the worker, and tends, too, to be less completely colored, frequently suggesting even in the physogastric state a more or less callow condition.

As in the case of the honeybee the queen of the stingless bees is a relatively hardy individual, with a normal expectancy of life that greatly exceeds that of the other members of the colony. Drory noted (1872b, p. 206; 1877, p. 115, footnote; Raveret-Wattel, 1872d, p. 689) that in the nest of *Melipona fasciata* variety *scutellaris* Latreille which he had under observation at Bordeaux, the queen was the last individual to succumb.

Rayment observed (1932a, p. 251; 1935, p. 534) that whenever a colony of *Trigona* died of starvation, it was the queen that remained alive to the end, "wandering over the desolate combs with one or two miserable attendant worker-bees." No doubt the queen is inherently geared for long life but it is to be remembered, too, that she is apt to receive preferential treatment, which in time of scarcity gives her a distinct advantage over the commoners of the hive. For example, Marianno (1911, p. 47) isolated two virgin queens and some workers of *Trigona* (*Tetragona*) *jaty* F. Smith and *Trigona* (*Trigona*) *fulviventris* Guérin and deprived them of all nutriment. The workers were the first to succumb but at every moment they aided the royal members, extending their tongue towards them, offering thus the few reserves of sustenance over which they had disposal.

Little satisfactory information is available regarding the egg laying capacity of the queen. According to the calculations of F. Müller (1875, p. 295) a queen of "mirim" [probably *Trigona* (*Plebeia*) *minima* Gribodo] laid about 150 eggs daily during the summer months, which would be at the rate of 4500 eggs per month. On the other hand, Tomaszek (1880, p. 60) rated the laying of what he interpreted as *Trigona lineata* (Lepeletier) at only 4000 eggs over the period of his observation, which covered about four months. In contrast, the honeybee queen may at the period of maximum oviposition deposit as many as 1500 to 2000 eggs a day, and under special favoring conditions provided by the beekeeper her rate may even be accelerated to 5000 eggs a day. However, in early spring and late fall even *Apis* may lay no more than a few eggs daily (Phillips, 1928, p. 48). The great disparity in the populations of stingless bee colonies according to the species seems to point to similar contrasts in the egg laying rate of the respective queens.

The fact that in the nests of stingless bees the cells from which will issue the commoners of the state are undifferentiated raises the question as to the particular stimulus that induces the queen to lay in one case an egg that will develop into a worker and in another case an egg that will produce a male. In the genus *Melipona* the interpretation becomes still more complex and baffling because in

that genus even the cell of the queen is undifferentiated.

MALE

The male of *Trigona* and of *Lestrimelitta* tends to approximate in size the conspecific worker, while in *Melipona* it is comparable in size not only to the worker but also to the virgin queen. In all three genera, the head of the male is somewhat smaller than that of the worker; the eyes are a little wider and more emphatically convergent below; the malar space is always shorter, sometimes reduced to the vanishing point. The facial quadrangle tends to be narrower than in the worker, being particularly reduced below, but above, too, the space is narrower than is the case in the worker, with the result that each lateral ocellus tends to be much closer to the nearest compound eye than in the worker caste. The flagellum, consisting of 12 joints, is longer than in the conspecific worker, but the scape is shorter than in that caste, although, in the case of *Lestrimelitta limão* (F. Smith) at least, the difference is barely traceable; frequently the flagellum tapers somewhat towards the apical extremity. The face is more maculated in many forms than is that of the conspecific worker and particularly is this true of the clypeus, but some males, especially within the subgenus *Trigona*, are unicolorous, as is the worker, and without ornamentation.

The thorax is sometimes a trifle more elongate than in the worker.

The tibiae of the hind legs are as a rule narrower than in the worker and lack a comb anteriorly at the apex of their outer side and the dense row of spines or spine-like hairs along the inner side of their apical edge, an equipment found in workers of *Melipona* and *Trigona*. Usually these tibiae have the hairs along their posterior rim less developed than is the case in the worker and often, too, they have hairs extending far down over the outer face of these tibiae, but such hairs may also be absent or nearly absent, for instance in the subgenus *Paratrigona*. The tarsal claws are cleft.

The wings usually resemble those of the worker.

The abdomen proper has seven visible tergites instead of six as in the worker and queen. The usually concealed basal part of

the tergites is sometimes more or less sculptured in case the exposed apical part is also sculptured, whereas in the conspecific worker this concealed area tends to be polished in contrast to the roughened apical area. The abdominal sternites are usually distinctive in structure, particularly the fifth, sixth, and seventh sternites (sometimes also those more basad), furnishing good characters for the separation of different species.

In the designation of the sternites of the abdomen I have followed the numbering adopted by Silvestri (1902b, pp. 121-174, pls. 1-3). In this numbering not only is the propodeum excluded from consideration by the designation of the first segment of the abdomen proper as segment 1, but the apparent sequence is recorded without attempt to estimate the possible loss or fusion of segments in the process of evolution. It has been my fear that to adopt any other course might hinder rather than aid in the identification of specimens, which is one of the prime functions of a description. For the guidance of the reader it should be pointed out, however, that what here are termed sternites 6 and 7 are by Snodgrass (1941, pp. 60-61, pl. 30, figs. H-O, pl. 31, figs. A-F) designated sternites 8 and 9, respectively. Sternite 7 of the present paper is called spatha in my monograph of the genus *Melipona* (1932, pl. 8, figs. C, H, L, pl. 9, figs. B, F, J, N, pl. 10, figs. B, E).

There are differences between male and worker, but there are also resemblances.

Males are usually poorly represented in collections. Among the 40 species that Lepeletier stated (1825, p. 710) he had described, there was only one male, and that one could not be referred to any species then known. Even where there are large series of workers in collections, the male is often lacking and indeed in the case of a number of described forms is still unknown. It is usually only when nest material is available (and not always even then) that males are present in adequate number; yet sometimes males congregate in fairly large assemblies outside the nest. (See in this connection the section on communal flight activities, p. 56, and, for further information about the male, the sections on wax production and a discussion of the role of the male, p. 43, protandry, p. 48, and the slaughter of the drones, p. 55.)

PRE-ADULT STAGES

The period required for the completion of the pre-adult stages in stingless bees has been variously estimated by different observers. According to Drory (1873a, p. xxxiii), who cited the observations of Brunet, the stingless bee known in Bahia as "urussus" (presumably *Melipona fasciata* variety *scutellaris* Latreille) requires for its complete development from egg to adult at least 46 days and a mean temperature of 27° C. This estimate is very close to that which Tomaschek (1880, p. 61) gives as the required time of development (about seven weeks) for what he designated *lineata*. Both of these estimates transcend the time required, according to F. Müller (1874b, p. 103), for the maturation of "mirim" [presumably *Trigona* (*Plebeia*) *minima* Gribodo], which required from five to six weeks. An average of 36 days was the time required for maturation according to the calculations of Buttel-Reepen (1903a, p. 135). In contrast to this rather brief time span is the calculation of Hockings (1884, p. 150) that the Australian *Trigona carbonaria* F. Smith and *Trigona cassiae* Cockerell require three months from egg stage to adult. Rayment (1932b, p. 11; 1935, p. 541), cited a later communication of Hockings to the effect that 70 days was the required period and then went on to state as his own view that "the time taken to reach maturity varies considerably, ranging between 50 and 70 days."

On the other hand George (1934, p. 5), who made a painstaking study of the developmental stages of the Old World *Trigona* (*Tetragona*) *iridipennis* F. Smith, assigned a period of no more than three to three and one-half weeks for the completion of the transition from egg to adult. This estimate much more nearly approximates the time required in the case of the honeybee to reach maturity. Twenty-one days suffice on the average for the worker of *Apis* to attain adult status, the first three being passed in the egg, the next six as a larva, and the last 12 as a pupa. The period of development for the queen of the honeybee is even less than for the worker, being telescoped into about 16 days, but the development of the male is more retarded, requiring on an average about 24 days.

In the absence of mention of a particular

caste, the different maturation periods cited above for stingless bees may be assumed, I think, to apply to the worker, by far the most prevalent individual in any normally constituted colony. Rayment (1932a, p. 249) has this to say about the time covered in the pre-adult development of the queen: "In one colony of *T. cassiae* that I studied, the sole young queen had only just started to deposit eggs, but notwithstanding this, I was able to discover a queen-cell that contained only a very young larva which did not reach its full development until two months later."

"Fritz" Müller (1878, p. 231), who had under observation colonies of several species of Brazilian stingless bees, came to the conclusion that *Melipona* had this in common with the Old World honeybee: the queens of both develop more quickly and the drones more slowly than do the conspecific workers.

Larval anatomy and metamorphosis were studied by George in the case of *Trigona* (*Tetragona*) *iridipennis* F. Smith, and George's summary and conclusion (1934, p. 12), indicating the special features brought out in his investigation, may be quoted herewith: "(a) A few fat cells become modified as excretory cells during metamorphosis (pronephrocytes); (b) The adult oenocytes are formed from the hypodermis of the pupa; (c) The larval nerve cord with three ganglia in the thorax and eight in the abdomen becomes modified into a cord with two ganglia in the thorax and five in the abdomen when the adult condition is reached. The composite nature of the penultimate abdominal ganglion is established on anatomical and developmental grounds; (d) The formation of the female efferent system has also been studied, and it has been found that it takes place on the same lines as in Homoptera (George and Metcalfe), and Orthoptera (Nel). The accessory glands (the poison glands) are present though the sting has become nonfunctional. It has been inferred therefrom that these glands are ancient structures of physiological importance in connection with the reproductive habits of the animal and their function as poison glands is a secondary modification. Such glands arising from the 9th abdominal segment are present in Homoptera and Orthoptera, etc."

A pair of silk glands was noted by George

ventral to, and on either side of, the alimentary canal, extending posteriorly to the eighth abdominal segment. Under metamorphosis these silk glands undergo complete histolysis and disappear entirely.

In an earlier paper (1933, pp. 58-61) on excretion in *iridipennis* during metamorphosis, George called attention to certain large cells that make their appearance among the fat cells of the abdominal region after the larvae defecate and in turn disintegrate in the adult. These cells, because of their rather striking resemblance to the nephrocytes, he named pronephrocytes. The appearance of these cells during the prepupal stage and the presence in the cytoplasm of what were interpreted both by George and Keilin, to whom the slides of these cells were submitted, as excretory products led George to the conclusion that the pronephrocytes are "specialized cells called in at the interval between the histolysis of the larval Malpighian tubules and the appearance of the imaginal ones, to perform the vital function of excretion."

CALLOWS

As the callow takes on the coloration of the adult, the transformation in the different body parts of the bee is not uniform. Some parts assume the final coloration more rapidly than do others. Yet opinions differ as to those parts that are the more enterprising in achieving the change and those that are the more resistant to it.

Stadelmann (1895, p. 621) stated of the African *Trigona erythra* variety *togoënsis* that on leaving the cell the callow is light brown, that the abdomen is the first part to become gradually darker, that then the head follows, while the thorax and legs still retain their light yellow coloration for some time. Rayment, too, maintained that "the abdomen of *Trigona* is the first to blacken" (1935, p. 531) although the context leads me to believe that his generalization may have been based on the study of only the Australian *cassiae* and *carbonaria*.

In contrast with the observation that the deepening of the coloration starts with the abdomen is that of Schulz (1905c, p. 141), who, in commenting on callows of *Trigona* (*Partamona*) *testacea* variety *cupira* F. Smith,

stated that the black pigmentation affected first the head and the thorax (with the exception of the scutellum), then the abdomen, and last of all the scutellum. The transition is from pure white through yellowish brown to wholly black. In a series before me of the rather closely related *Trigona* (*Partamona*) *testacea* variety *helleri* Friese the abdomen, scutellum, and clypeus seem to retain the coloration of the callow the longest.

A curious observation on the attainment of full body coloration is contributed by Wheeler (1913, p. 5), who in the case of *Trigona* (*Tetragona*) *nigra* variety *paupera* (Provancher) noted that, whereas in life the narrow abdomen of this bee is apt to be a peculiar livid white color (such specimens are usually interpreted as callows), in dried specimens the abdomen "often turns black like the remainder of the body." The variety *paupera* is particularly prone to have in the callow an abdomen wholly or largely white, and such callow specimens, examined without benefit of intergrading specimens in a series, might well prompt the belief that they constitute an independent variety.¹ That is what, I believe, happened in the case of the Indo-Malayan *Trigona* (*Tetragona*) *fusco-balteata* Cameron, which in my opinion (1939c, p. 107) is probably merely a callow, with more or less pale abdomen, of the fully darkened bee subsequently described by Cockerell as *atomella* (1919a, pp. 243-244).

Among the body parts in my estimation generally most resistant to nigrification are, in addition to frequently the abdomen, the following: the clypeus, supraclypeus, labrum, lower end of genal area, sometimes the inner orbit of the eyes, and mandibles, the scutellum, the propodeum, to a lesser degree the pleura, and in some instances (more especially in the subgenus *Trigona*) the hind tibiae.

¹ In a recent paper Michener (1946, pp. 188-189) stated that in Old Panama all individuals of *paupera* seen at the nests had a black abdomen. On the other hand, all individuals collected for him by Dr. Harold Trapido from a nest that was located between the walls of a house in Juan Mina, Canal Zone, were differentiated by having the abdomen whitish dorsally. From this experience Michener concluded that "it seems possible that there is a genetic basis for the color differences, some colonies consisting wholly of black specimens, some consisting wholly of individuals with white, and some colonies being mixed."

It will be noted that several of these areas, especially the clypeus and the scutellum, are areas that in many species of stingless bees are normally pale in any event, and the retardation of the darkening of these parts is therefore interesting.

Among the callow specimens before me are quite a number (more particularly in the subgenus *Trigona*) that have on the clypeus two reddish marks that in shape and position somewhat suggest the clypeal maculations found in many forms of the subgenus *Partamona*. Callows of *Trigona* (*Trigona*) *fulviventr* variety *fulviventr* Guérin often have two subparallel black longitudinal stripes on their yellow clypeus. Thus certain fundamental patterns, frequently lost in the fully colored insect, are, one is tempted to believe, sometimes retained for a time in the callow.

How color patterns that characterize the callows of a given species sometimes tend to approximate the mature coloration of another and only distantly related species is well illustrated in the case of *Trigona* (*Cephalotrigona*) *capitata* variety *zexmeniae* Cockerell, the mesonotum of which has in the callow a coloration and design almost interchangeable with that of the adult *Scaptotrigona* that Friese designated *hellwegeri*. It is, furthermore, remarkable that in both of these bees the scutellum is black, which is at variance with the usual condition, at least in callows, in which the scutellum more than the mesonotum resists nigrification. (See p. 458.)

GYNANDROMORPHS

A lateral gynandromorph of *Trigona* (*Partamona*) *testacea* variety *testacea* (Klug) was described by me (1929, pp. 145-150, pl. 6) and was figured in the same paper by Mrs. E. L. Beutenmüller. Only this single specimen out of a total of 400 from the same nest evidenced sexual abnormality. Seemingly the phenomenon is a rare one. I recall no other instance among the Meliponidae, but it is always possible that at some time a nest of *Trigona* or of *Melipona* will be found comparable to the famous hive of honeybees owned by Engster of Constanx in the sixties of the last century, in which no fewer than 87 of these strange creatures combining characters of both sexes were available for study.

ENEMIES AND DEFENSE AGAINST ENEMIES

ARE THE STINGLESS BEES STINGLESS?

The Meliponidae are universally known as stingless bees, and this is the fact in so far as their failure to inflict wounds by means of a sting is concerned. But, as H. von Ihering (1886, pp. 177-188) indicated on the basis of a study of 10 different species of *Melipona* and *Trigona*, the sting is atrophied rather than absent. The base of the sting and the attached skeletal parts, according to von Ihering, have been preserved in a recognizable manner although with variable distinctness, but the poison apparatus and the tip of the sting have dwindled away. Fifty years previously Latreille in a letter to Pierre Huber (Huber, 1839, pp. 8-9) commented on some specimens of *Melipona beecheii* Bennett that Huber had sent him for examination and confirmed the impression of Huber that, if a sting exists, it must be "very small, rudimentary, and inoffensive." Yet at an earlier date Latreille (1812b, p. 263) disputed the belief that stingless bees are stingless and contended that probably the sting was small rather than absent, a conclusion not too greatly at variance with its actual atrophy.

The inability of the worker of Meliponidae to sting was established at an early date. Spinola was the first, however, to confirm through dissection that the queen likewise is devoid of an effective stinging mechanism (1842b, p. 267). His observations were made on a queen of *Melipona beecheii* variety *fulvipes* Guérin. The vestiges of the sting are, however, said to be more pronounced in the queen than in the worker (George, 1934, p. 4).

The Meliponidae, alone among the bees, approximate the condition of stinglessness found in ants of the subfamilies Formicinae (Camponotinae) and Dolichoderinae. Sometimes, however, they simulate the act of stinging by pressing the tip of their abdomen against the victim, now and then with such strength that, as Engelhardt describes it (1909, p. 45), "the dull pressure of it could be distinctly felt."

Some years before the publication of Darwin's "Origin of species" and at a time when the conception was still prevalent that nature existed only for the benefit of man, Jesse

(1854, p. 305) could speculate thus regarding the absence of the sting in Meliponidae as contrasted with the armed condition of *Apis*: "One would at first suppose that they [the stings] were equally required for the protection of the insect in both: but we know that in hot weather bees are extremely irascible; if, therefore they were furnished with stings in the West Indies, they would probably attack everything which came near them, and thus become so intolerable a nuisance to man, that their utility would not compensate for it."

Dismissing this anthropocentric concept, is there anything to be said from the bee's standpoint regarding the advantages of stinglessness? At first thought, the Meliponidae would seem to have been treated unkindly by Nature, deprived as they are of a weapon of defense that is assumed to be helpful to stinging Hymenoptera. But is it possible that there are compensations in this loss?

In a group like the sphecoid wasps, from which it seems probable the bees were derived, the sting has a significance that transcends its use as an instrument of aggression or of defense. For these wasps apply their sting primarily not against actual or potential enemies but for paralyzing their prey (insects and in some cases spiders) on which their young are dependent for their very existence. The bees, on the other hand, dedicated to an exploitation of nectar and pollen, have no requirement for a deadly instrument as they pillage the floral bloom. But even in its limited function of combative weapon, is the sting an effective tool? Those who have been stung will be inclined to answer "yes." However, the bee's point of view is also entitled to be consulted. For the honeybee the act of stinging is usually fatal and the same comment probably applies to certain of the social wasps (Vespidae), which although further removed than are the bees from the sphecoid wasps, nevertheless, like them, belong to the aculeate or stinging Hymenoptera. Some species of these wasps, it is known, suffer mutilation in the act of stinging. Phisalix (1922, pp. 428-429), who has written an embracing account of poisonous animals

and their poisons, noted that in bees the sting is "ill adapted to the function of attack and of defense that is generally attributed to it." This author then went on to say that: "From this point of view, it [the sting] is rather hindering than helpful; and in consequence should by rights have disappeared if it did not have another role, namely that of aseptizing the honey and the hive."

It may be, therefore, that what we have looked upon as a structural degeneration in the stingless bees, the atrophy of their sting, is merely a readjustment to achieve a more perfectly functioning organism. According to this conception stingless bees, through their very stinglessness, are pointing the way to a higher development, while the other bees are still encumbered laggards, dragging about with them chains that imperfectly bind them to a past from which they are not yet fully emancipated.

The theory just outlined is tempting. Yet before accepting it, the fact must be weighed that it is not only the sting but the poison glands as well that have undergone degeneration in some, at least, of the stingless bees, although in other instances (the subgenus *Oxytrigona*, for instance) there are still potent reserves of poison. Unfortunately, H. von Ihering (1886, pp. 177-188) does not make complete mention of the 10 species of Meliponidae he examined in his search for traces of a sting and the associated poison apparatus, but one is forced to conclude that among them were probably no members of the subgenus *Oxytrigona*, presently to be commented on in greater detail. At least the failure to find functioning poison glands in the bees of this subgenus would be startling in view of the outpourings of caustic fluid with which *Oxytrigona* makes effective its attacks. But if *Oxytrigona* illustrates the replacement of one type of defense by another even more potent, the majority of stingless bees may possibly have little poison at their disposal even for safeguarding their honey from corruption, much less for chemical warfare. Petit (1891, p. 238) maintained that the absence in the Meliponidae of the sting, the agent of transfer of the formic acid, had led to the suppression of this secretion, which "alone permits the honey to be preserved." On the other hand, Peckolt (cited by Phisalix,

1922, p. 428) found a small percentage of formic acid in the honey of *Trigona* (*Trigona*) *ruficrus* (Latreille), and Phisalix (1922, p. 428) stated it as a certainty that the digestive glands of bees are capable of secreting toxic substances as ingredients of the honey. Moreover, George (1934, p. 12), who made a painstaking study of *Trigona iridipennis*, found that in that species, at least, the poison glands "are present even though the sting has become non-functional." George drew the conclusion that antecedent to their function as poison glands these structures had a physiological role in connection with the reproductive habits of the insect.

The reasons for the dwindling of the sting and its functional desuetude still elude one. Certainly there would seem nothing in the biology of the Meliponidae that required such a drastic change of structure in conformity with a given mode of life; nor, from another angle, do the peculiarities of their communal existence seem to have been conditioned to any perceptible degree by their deprivation of a sting. All we can really say with safety is that the Meliponidae lack as a means of aggression and of defense the weapon most commonly associated with bees in general.

DEFENSIVE WEAPONS AND METHODS OF THE INDIVIDUAL BEE

Incapable of stinging though they be, the Meliponidae are by no means devoid of other means of defense and of aggression, too. In numbers they frequently hurl themselves upon those who venture indiscreetly near their nest, and crawl into nostrils, ears, hair, and eyes, in addition to lodging on the hands or any exposed part of the body. Their annoying penetration of the hair of the scalp or of the beard has earned them in southern Brazil the name of "hair twisters" or "curl papers" ("torce cabellos" in Portuguese and "Haarwickler" in German). The Kekchi Indians of Alta Vera Paz, Guatemala, regularly wrap a cloth about their heads when pillaging a stingless bee nest in order to protect their hair from invasion (Sapper, 1935, p. 184). *Trigona* (*Hypotrigona*) *duckei* Friese (commonly asserted to be the smallest bee, although this distinction is possibly challenged by a tiny member of the genus *Turnerella*) was described from specimens

that crawled into the eyes of an entomologist. In fact, a common name for this bee in the State of Matto Grosso, Brazil, is "lambe olhos" or eye licker (Ducke, 1925, p. 342). An amusing if fantastic interpretation of the action of an African species—probably a stingless bee—is supplied by Hughes (1933, p. 335), who stated that, "These tiny black bees, searching for a suitable knot hole for a nest, will often explore the aperture of one's ear to see how it might suit their purpose."

In the State of Paraná, Brazil, Bigg-Wither (1878, p. 276) found what he referred to as "mirim" [probably *Trigona* (*Plebeia*) *minima* Gribodo] so abundant and so persistent that "it is no exaggeration to say that a person might kill fifty a minute on the back of his hand, for five consecutive hours during the day." Bigg-Wither did not apparently give practical demonstration of the truth or falsity of this calculation, possibly because, as he intimates in another sentence, the presence of the *Trigona* tended to reduce the space available to mosquitoes, thus making the stingless bees the lesser of two evils. Undoubtedly the bees were numerous, but it is easy to overestimate their abundance when one is subjected to annoying attacks.

Such mass attacks upon the victim would be sufficiently disagreeable if they involved no more than a perambulatory penetration of the recesses of his physiognomy, but as a rule the bees inflict as well little nips and bites with their usually more or less toothed mandibles and the cumulative effect of such bites is often far from pleasant. Species differ, however, very greatly in aggressiveness. One South American species was named *Trigona timida* by Silvestri (1902b, pp. 163–164, pl. 3, figs. 47, 48) because of its fearsome behavior. Some species are so docile that they have earned the name of "angelitos" or little angels, bestowed upon them by our Latin American neighbors (Gosse, 1851, p. 464; von Humboldt, 1811, p. 240; 1817, p. 257; 1852, p. 434; Wheeler, 1923, p. 121). Yet von Humboldt was a little skeptical of their celestial aloofness and, although assured by his guides in Venezuela that the "little angels" would attempt to defend themselves "only when irritated by being seized by the legs," he was not tempted to put them to the test, partly doubtless because he mistakenly

believed that, though reputedly stingless, they were capable of inflicting a feeble incision. In Colombia, in addition to being designated "little angels," meliponid bees bear the less flattering title of "abejas bobas" (Raveret-Wattel, 1875, p. 738). Just as we apply the term "fool hen" to a bird that shows an unjustified confidence in the good intentions of man, so these bees are classified as "foolish" because of their inoffensive behavior. Salt (1929, p. 442) indicated that a similar name, "mosca boba," was applied to *Trigona* (*Cephalotrigona*) *capitata* variety *zemeniae* Cockerell in the Santa Marta region of Colombia because of the complacent behavior of these bees in permitting their nest to be emptied of the "ample stores of excellent honey."

Even those stingless bees that attack will often desert their victim as soon as he has moved away an adequate distance from the nest. Thus *Trigona* (*Scaptotrigona*) *pectoralis* Dalla Torre desisted from attack, according to Wheeler (1913, pp. 5, 6), as soon as the victim moved 20 feet from the nest site, and the same observer noted that *Trigona* (*Scaptotrigona*) *bipunctata* variety *wheeleri* Cockerell flew off when he had walked only a few paces from the colony these bees were defending. *Trigona* (*Oxytrigona*) *tataira* variety *mediorufa* Cockerell, a more aggressive bee than either of the other two species mentioned, nevertheless deserted its victim at 30 feet from the nest (Wheeler, 1913, p. 8). These instances (all cited from a single observer) tend to show that the attacks, however unpleasant, are usually of limited duration provided the person attacked retreats from the scene. Salt, however, had a different experience (1929, p. 440). Attacking individuals of *Trigona* (*Trigona*) *amalihea* (Olivier), he stated, "clung in the folds of my clothes and bit at intervals until I had picked off each one individually." Similarly H. Fleming while in Venezuela found "extremely ferocious" a large colony of these bees located "in a very large nest at the base of an extremely large tree." Twice, he wrote me, he was attacked, on one occasion from a distance of 10 yards and on another occasion at a distance of 20 yards.

Ground nesting forms are in general reputed to be timid and relatively innocuous;

species that build exposed nests, on the other hand, tend to be unpleasantly demonstrative. Nevertheless, Engelhardt had a contrary experience in Guatemala, for he asserted (1909, p. 45): "Some of the bees, especially those that build clay nests under ground, displayed a fierce disposition on being disturbed, attacking, seemingly with preference, eyes, ears and nose of the disturber, and even crawling under the clothing." So one has to be cautious in making generalizations. Even in a single subgenus, like *Trigona*, such commonly aggressive species as *amalihea* and *ruficrus* are offset by a docile form like *fulviventris*. I have stood beside a nest of *fulviventris* for long stretches of time with my face close to the flight tube without ever being molested.

Among the species that are particularly combative is *Trigona* (*Tetragona*) *heideri* Friese. Ducke (1916, p. 70; 1925, p. 383) indicated that *heideri*, of all the stingless bees whose colonies were known to him, was by far the most aggressive species and in a footnote (1925, p. 383) he added that *heideri* will attack even though the victim be many meters distant from the nest and even though he has in no way molested the inmates. Roman (cited by Alfken, 1930b, p. 8) also paid tribute to the biting capability of this bee. The unusually strong teeth on the inner side of the mandible of *heideri*, resembling the armature of certain Indo-Malayan stingless bees, such as *Trigona* (*Tetragona*) *haematoptera* Cockerell and *Trigona* (*Tetragona*) *fimbriata* F. Smith and its varieties, seem a particularly potent weapon for aggressive use.

Another species that ranks as one of the most belligerent is the above-mentioned *Trigona* (*Trigona*) *ruficrus* (Latreille). Undissenting denunciation of this bee as one of the most easily provoked and aggressive of the whole group is indulged in by all who have suffered its attacks. Peckolt (1894, p. 224) even affirmed that, instead of retreating before tobacco smoke as did all other stingless bees with which he had experience, *ruficrus* alone was provoked to combative fury by a whiff of the smoke.

Among those who have given too free a rein to their fancy in describing the ferocity of some stingless bees mention may be made

of Malaney (1930, p. 588), who stated that "their method of defense is to butt like a goat," adding "the whole colony will attack a foe and hit like a hailstorm."

Although most *Trigona* employ only mandibles as weapons, there is one group (the subgenus *Oxytrigona*) which makes itself even more effectively unpleasant by depositing a caustic fluid. The spots where the bees deposit their "fire" may remain sensitive for days, even incapacitating the victim, and the evidences of searing may still be traceable at the end of three weeks (Drory, 1873a, p. xxxii), or even after two months or more according to the subsequent personal experience of Drory (1877, p. 148). Brunet, it is claimed, had to take to his bed for eight weeks after an attack (Drory, 1874, p. 285). So disconcerting is the method of attack, making calm observation difficult under the circumstances, that it is perhaps not surprising to find divergence of opinion as to the origin of the fluid. One group of hymenopterists, including those actually attacked as well as those whose conclusions are based on the experiences of others, holds to the viewpoint that the fluid is injected from the mouth in the act of biting or subsequent thereto (Drory, 1873a, p. xxxii; 1874, p. 285; 1877, p. 146; Silvestri 1902b, pp. 144-145; H. von Ihering, 1903, p. 206; Marianno, 1911, p. 85). On the other hand, Coelho de Scabra (1799, pp. 101, 103), Saint-Hilaire (1830, p. 372), Raveret-Wattel (1872b, p. 421), Peckolt (1893, p. 580; 1894, p. 225), and Wheeler (1913, pp. 8-9) were of the opinion that the fluid was emitted not from the mouth but from the anal end of the body, thus indicating a parallelism in defense methods between these bees of the subgenus *Oxytrigona* and ants of the subfamily Formicinae. It is possible, too, that von Spix and von Martius (1828, p. 542), who erroneously ascribed the skin irritation produced by these bees to a sting, really were basing their impression upon the contact of the tip of the abdomen with the victim and hence should be ranked with Coelho de Scabra, Saint-Hilaire, Raveret-Wattel, Peckolt, and Wheeler in support of the viewpoint that the poison proceeds from anal rather than from salivary glands. Be it mentioned in this connection that stingless bees of other subgenera some-

times simulate the act of stinging even though they are incapable of inflicting a wound or have no irritating fluid to discharge. Bristowe (1925, p. 479) quaintly described this ineffectual gesture as "digging their harmless tails into me."

So painful is the irritation produced by an attack of bees of the subgenus *Oxytrigona* that these bees bear the expressive popular name in Brazil of "cacafofo" or "cagafofo," variously translated as excrement of fire (Saint-Hilaire, 1830, p. 374), spit fire (H. Müller, 1874, p. 32), and fire defecator (Wheeler, 1913, p. 8), possibly in conformity with the translator's adherence to one or to the other of the two conflicting theories as to the point of emission of the caustic fluid. The specific name, too, *tataira*, which is merely the adaptation of an aboriginal name, probably was conferred on these bees out of regard for the fiery nature of their attack, for, according to H. von Ihering (1903, p. 277) and Bertoni (1911, p. 144) "tata" means fire and the name for the bee in the Tupi or Guaraní language is "ei-tata" or "eira-tata," an inversion of *tata-ira*. Literally *tataira* means "fire honey" (H. von Ihering, 1903, p. 277). A different explanation is offered, however, by Saint-Hilaire (1830, p. 374), who believed that *tataira* stemmed from "atura," meaning red, and was conferred upon the bee because of its color. There is, it should be said, much range of color from variety to variety within *Oxytrigona*.

There can be no question that members of the subgenus *Oxytrigona* emit a fluid that is strongly irritating to the skin. Too many have experienced this painful method of attack, which long antedates man's perfection of chemical warfare, to leave room for doubt. On the other hand, it is a little puzzling to learn from Drory (1873d, p. 61) that "the greater number of species of *Melipona*" at the time of biting secrete in their mouth "a kind of yellow or brown saliva of a very strong and disagreeable odor." Drory does not actually say that the secretion is injected with the bite, and the passage receives some clarification, I think, in a later publication by the same author (1877, p. 147). In this later article Drory mentioned *Melipona postica* and *Melipona muscaria* (both of which are *Trigona*) as crawling into the hair of the head,

beard, eyelashes, and the ears and spreading over these areas "an odor very penetrating but not insupportable." Undoubtedly it is something of this sort that Drory had reference to in his earlier paper rather than the implication that the bite of most "*Melipona*" was made more severe through the simultaneous discharge of some fluid.

Yet, while Drory's statement was applied to "the greater number of species of *Melipona*," there is at least one stingless bee, *Trigona* (*Trigona*) *ruficrus* (Latreille), that Peckolt (1894, p. 223) definitely accused of discharging a sticky fluid as it makes its way through the fur of animals or the hair of men. Peckolt stated that the discharge was so effective that even the bee itself is sometimes made fast to its victim by its own entangling secretion. Happily, unlike the fluid discharged by the *Oxytrigona*, the sticky material allegedly released by *ruficrus* does not produce painful effects. Peckolt's account is in need of substantiation. One wonders whether the sticky material in this case was not resinous material gathered in foraging that still adhered to the hind legs and glued the bee to the hairs of her victim as she sought her way through the dense hirsute tangle. Williams (1928a, p. 172) stated that in the island of Trinidad the expressive name "tar babies" is often applied to those stingless bees that "get into one's hair and daub it with their gummy legs." Although *ruficrus* is not known to occur in Trinidad, the effect of the attack of Williams' bees seems much like that recorded by Peckolt for *ruficrus*, and the sticky material would seem possibly to be of similar origin in both cases.

The methods of defense and of aggression thus far indicated are supplemented by yet another device, of use mainly against intruders into the fastnesses of the nest. Drory (1872b, p. 174; 1873d, p. 70; cited by Raveret-Wattel, 1872d, pp. 684-685), to whom we owe so many interesting observations regarding the behavior of stingless bees, has placed us under indebtedness also for this instance. Drory's accounts, which I have had the opportunity of reading, are rare documents, and this doubtless explains the fact that the incident he records has not received more general attention. However, it has been summarized by Girard (1875a, p.

570) and also by Tomaschek (1880, p. 63). At one time during his observations on a colony of *Melipona fasciata* variety *scutellaris* Latreille, which had been transplanted from Brazil to Bordeaux, Drory discovered an enterprising wasp which had succeeded in making its way through the tunnel of wax that leads to the heart of the nest and thence had penetrated on to the honey pots. But there was no silken cord of Ariadne to conduct this intruder back to the outer world and presently she was attacked with fury by five or six members of the hive. Drory expected to see at least one or more of the unarmed bees penetrated by the sting of the wasp and rendered *hors de combat*. Instead, when the contestants disengaged, it was the wasp that was in difficulty. On the front of her head was a small sticky particle, clear and transparent, which she was endeavoring to remove with what Drory described as feverish anxiety. But the more she used her legs to free herself of the encumbrance, the more these became fastened to her head, and in the end, with her wings similarly attached, she came to resemble a round bullet. Two or three days later her desiccated remains, cut to pieces, were carried out of the nest by the bees.

A very similar incident, in which likewise a wasp is overpowered and, if one may so express it, glued to death is told by J. Pelletan (cited by Raveret-Wattel, 1875, pp. 747-748). One wonders indeed whether the inspiration of the account is not Drory's own narrative. However, Pelletan adds one or two details, which may be embellishments, including the assertion that the material that is smeared over the intruder is wax or propolis, whereas Drory (cited by Raveret-Wattel, 1872d, p. 685) had merely alluded in a footnote to the probability of its being propolis. Another possibility is that the sticky substance, "clear and transparent," was honey. The species of stingless bee is not mentioned by Pelletan, but I suspect it is *Melipona fasciata* variety *scutellaris* Latreille, for Pelletan's article from which the citation is made was devoted to the stingless bees on exhibition in Paris during 1874, and of the two hives thus exhibited *scutellaris* was one.

It is likely that this peculiar method of disposing of an intruder is not restricted

among the *Melipona* to *scutellaris* alone, for *scutellaris* is a very close relative of a great many other members of the genus *Melipona*. In fact, its relationship is so close to these that I regard *scutellaris* merely as a variety or subspecies of the widely distributed and variable *Melipona fasciata* Latreille. It is hard to believe that within this group of intergrading forms the interesting habit manifested by *scutellaris* does not repeat itself. Indeed, what gives strength to this belief is the fact that the same method of aggression or defense has been observed in the case also of an Australian *Trigona*. Thus another member of the Meliponidae belonging to a different hemisphere proves to be schooled in the same technique. My authority is Hockings (1884, p. 152), who gives the following interesting account of the defensive methods of the *Trigona* species popularly known as "kootchar" (*Trigona cassiae* Cockerell): "Should a strange insect be placed in their hive they follow it in a crowd, continuously placing small globules of gummy matter on its body; this substance seems to be extruded from their mouths and has a slightly greenish colour when wet, and soon becomes very hard, so that the stranger in time is unable to move, and it is then firmly fastened down and quietly dismembered, the parts being cast from the hive."

Although I have been unable to track down other instances of this strange method of warfare among the stingless bees, it may be noted that Ducke (1916, p. 70; 1925, p. 383) accused *Trigona* (*Tetragona*) *heideri* Friese of soiling its victim (in this case a human being) with a resin-like substance. To a human being such an attack would be merely unpleasant, but in the case of a small creature the application of a sticky substance to its small body might well lead to the same results as those observed by Drory in the case of *Melipona fasciata* variety *scutellaris* Latreille and those noted by Hockings in the case of the "kootchar." On the other hand, one might perhaps with nearly equal plausibility contend that these sticky deposits of *heideri* are, like those of the "tar babies" discussed on an earlier page, the accidental daubing from a gummy leg rather than a deliberate attempt to embarrass the enemy.

The flypaper method of rendering the op-

ponent impotent, as recorded for *Melipona fasciata* variety *scutellaris* Latreille and for *Trigona cassiae* Cockerell, is the more interesting because it is shared by at least one of the bumblebees, thus demonstrating how history repeats itself within the social Hymenoptera or indeed among social insects in general. Both in inception and in result the method recorded of *scutellaris* and "koot-char" is reminiscent of the technique of nest defense reported by Plath (1934, pp. 75-77) for *Bombus fervidus* (Fabricius). Of this bumble bee Plath wrote:

"On July 24, 1921, I noticed a disheveled *Psithyrus laboriosus* female crawling out from the nest-material of a colony of *Bombus fervidus*. She was wet all over, her pile being matted against the integument by a sticky liquid. On the same day a worker of a colony of *Bombus impatiens* which had been placed near the *fervidus* colony the preceding evening was found sitting near the entrance to her nest, and, like the *Psithyrus* female, she too was completely covered with a sticky liquid. Whenever this worker attempted to enter her nest, she was immediately attacked and driven back by the other members of the colony. The reason for this strange behavior and the source of the sticky liquid, which I was at first unable to account for, were disclosed a few days later.

"On July 27, I introduced a *Psithyrus laboriosus* female into a nest of *Bombus fervidus*, and was surprised to find that the workers, instead of creating a furore and killing the *Psithyrus*, as do the workers of *Bombus impatiens*, remained calm and resorted to a more peaceful, but equally effective, method of expelling the intruder. About a dozen workers gathered around the *Psithyrus*, and, after stealthily approaching a little nearer, each one placed a small droplet of liquid on the intruder with her mouth. The *Psithyrus* did not seem to relish this performance, and slowly left the comb, apparently seeking to hide herself. A number of workers followed her, and from time to time added more liquid, until she was as wet as the *Psithyrus* female and *Bombus* worker referred to above. The experiment was repeated with other *fervidus* colonies, and was later demonstrated before the Cambridge Entomological Club. The members of the

club were shown the very different behavior of a colony of *Bombus impatiens* under similar conditions.

"From July 27 to September 24, a considerable number of experiments were carried out in order to determine how colonies of *Bombus fervidus* react to other intruders. These experiments may be summed up briefly as follows: At various times, a young female of *Psithyrus ashtoni* and workers of *Bombus affinis*, *Bombus bimaculatus*, and *Bombus impatiens* were placed in the *fervidus* nest. All were daubed with liquid by the *fervidus* workers in the manner described above, but when a worker from another *fervidus* colony was introduced, it was attacked with legs and mandibles, and no attempt was made to daub it. During these experiments, the following animals were also placed in the nest-box: (1) worker honeybee, (2) male of *Bombus impatiens*, (3) male of *Polistes pallipes*, (4) bluebottle fly, (5) drone fly, (6) dragon fly, (7) small cricket, (8) gypsy moth, (9) young frog, and (10) a mouse. All of these were stung to death with no attempt at daubing. A katydid, however, was first daubed and then stung to death."

Plath reached the conclusion that the liquid used in daubing certain intruders was honey. He never observed this method of combat in the case of any bumblebee other than *fervidus*.

We have digressed from our stingless bees lured by the kindred interest of the bumblebees, but before turning to other techniques of combat, let it be said in passing that the envelopment of an intruder with sticky material may even be applied to an inanimate object. The honeybee has been known thus to entomb things that violated its domestic sense of fitness, to the inclusion even of a dead lizard or a small snake (Phillips, 1928, p. 117). But the stingless bees, too, cover over and thus remove from sight and smell whatever gives them offense. For instance, E. T. Bennett recorded (1831, pp. 364-365), from notes supplied by Capt. F. W. Beechey, that an attempt was made to daub the portress of a stingless bee colony with paint, in order to differentiate her from any bee that might replace her in single guardianship of the entrance of the nest. The attempt was unsuccessful, and some paint was spilled about the

exterior of the nest in the course of these efforts to mark the dodging watchman. Thereupon, "a troop of bees was soon observed to advance towards the place, each individual bearing a small particle of wax or of propolis in his mandibles, which he deposited in his turn upon the soiled part of the wood. The little labourers then returned to the hive, and repeated the operation until a small pile rose above the blemished part, and completely relieved the inhabitants from its annoyance." The passage has distinct interest, but we trust no one will offer it in evidence of the useful role of the male in hives of stingless bees, as Bennett (and probably Beechey originally) seems in this instance merely to have fallen victim to a slovenly manner of speech, substituting "he" when he meant "she."

Biting into the wings of an insect adversary seems a not uncommon mode of combat adopted by at least certain stingless bees. *Trigona (Tetragona) jaty* F. Smith embeds its jaws in the wing of the vastly larger honeybee, and doubtless also copes in similar manner with adversaries more nearly its own size (H. Müller, 1875b, pp. 52-53). Several instances of this martial technique are recorded from Australia. G. Bennett noted that, where honeybee and *Trigona* clashed in combat, it was not always the *Trigona* that fought on unequal terms. He stressed the advantage that the stingless bees derive by cutting off the wings of their adversary at the same time that they avoid her sting (cited by Raveret-Wattel, 1875, p. 758). Bennett did not mention the species of *Trigona* employing this method of warfare beyond characterizing the bees as small and black. We know, however, to a certainty that *Trigona carbonaria* F. Smith, at least, has this way of attacking. Indeed, the observations of Rayment made on *carbonaria* (1932a, p. 248; 1935, p. 531) rather closely accord with those set down by Bennett in the case of the unnamed *Trigona*. Rayment forcibly introduced a specimen of *Trigona cassiae* Cockerell into a nest of *carbonaria*. The members of the invaded colony bit into the axillae of the wing of the *cassiae* and then steadily twisted the flight organ until the mutilated bee was incapable of using its wings, whereupon it was carried away and dropped at a distance from the hive. The

account Hockings gives (1884, p. 151) of the technique of attack adopted by the *carbonaria* he observed differs somewhat from that of Bennett and of Rayment. In addition to the wings the legs, too, were seized. The wings, instead of being twisted or severed, were, like the legs, held taut fully extended until the victim succumbed. Probably the method of combating the intruder is not wholly stereotyped, for Hockings also observed cases where in single combat gladiators of *carbonaria* seized the abdomen of the adversary.

There is possibly yet another way in which Nature has safeguarded at least certain members of the Meliponidae, although it is equally possible that it works to the injury of a given species. All the methods of defense thus far considered are deterrent to the aggressor because they involve injury or discomfort. The method now to be mentioned is superficially comparable to that of the pacifist: to curb the combativeness of a would-be aggressor by giving proof of complete harmlessness. "Playing 'possum'" was at one time believed to give a certain degree of immunity from attack, for what aggressor would not lose interest in an opponent if that opponent seemingly dropped dead? Many insects tend to become immobile when seized, notably carabid beetles. It has been recorded of the stingless bee, *Trigona (Tetragona) silvestrii* Friese, that, if it be touched or grasped, it, too, "feigns death" (H. von Ihering, 1912, p. 5).

MIMICRY

Mimicry is one of the ways in which, it is contended, various creatures escape their enemies. There are instances among the stingless bees where a given species resembles some other insect with which fundamentally it has little relationship. Thus the banded condition of the abdomen and the other maculations, as well as the general shape, of *Melipona interrupta* variety *grandis* Guérin tricked Packard (1869a, p. 59) into describing it as *Anihidium pictifrons*, notwithstanding the fact that Packard in his description set down such characters as "but one subcostal cell, and that faintly marked on the outer side," which should definitely have excluded it from the company of the anthidiine bees.

Not similarly misled but nevertheless impressed by the superficial resemblances that a *Melipona* from southern Brazil bore also to the anthidiines, Lepeletier (1836, p. 417) named his bee *Melipona anthidioides*.

In like manner Cresson (1878, p. 181), while recognizing his *perilampoides* as a *Trigona*, indicated by the choice of the specific name the curious resemblance that this insect has to certain members of the genus of parasitic wasps, *Perilampus*.

In the case of the maculated stingless bees a claim for protective mimicry can perhaps be made on the ground that, because so many of the stinging Hymenoptera wear a similar uniform of yellow stripes and bands, a certain advantage would be derived by those that, although they lacked a dagger, had donned this martial garb even if under false pretenses. But such a line of reasoning fails to explain why a great many species of stingless bees that are unicolorous (either wholly black or wholly yellow) nevertheless have been very successful if extent of range and abundance within the range are criteria of success.

In other cases, where superficial resemblances of one *Trigona* to another *Trigona* might seem to establish a cumulative protection on the ground that both are individually feared on account of their unpleasant habits, the contention is perhaps robbed of some of its significance by the fact that sometimes the resemblances are found in species that occupy geographic areas disconnected from each other.

In alluding to the fact that *Trigona* (*Scaura*) *longula* (Lepeletier) lives in the nests of termites, Marshall (1898, p. 145) was tempted to conclude that both the termites and the bees derived mutual benefit from the

association. He then went on to point out that *longula* is "a nearly colorless, almost transparent species whereas the other species are strongly colored." The premise is a false one, for *longula* is prevailingly black in the specimens of mature coloration, but even more misleading is the implication, if I interpret Marshall correctly, that this putative convergence of the coloration of bee and termite is helpful to each insect. It is obvious that the termite is helpful to the bee in providing a nest site for the latter, but the only way in which the bee can be helpful to the termite is in serving notice on possible enemies of the termite that the abode of the termites is now shared by a social insect of aggressive disposition and such notice is emphatic only if there is no chance that the bee will be mistaken for the termite.

Similarly I am unable to follow the reasoning of Marianno (1911, p. 53) who, in his discussion of the natural means of defense of stingless bees, seems to imply that *Trigona* (*Trigona*) *ruficrus* (Latreille) derives some advantage from the fact that its exposed nests so closely resemble those of arboreal termites that at a distance it is impossible to differentiate the nest of the bee from that of the termite. But surely, if either social insect is protected by this resemblance of abodes, it is the termite that profits from the mimicry, for *ruficrus* is a bee noted for its ferocity and any creature experiencing its aggressiveness might well be cautious in approaching a nest believed, however mistakenly, to house this combative insect.

In mimicry things are not altogether one-sided. While there are certain stingless bees that wear a disguise that has tricked some observers into believing them something that they are not, there are insects of other affilia-

PLATE 3

Flight tubes of *Lestrimelitta limão* (F. Smith). These bees make rather characteristic flight tubes to their nest, with stalactite-like extensions on the under side, but the range of variability is considerable.

1. Reproduction of a flight tube figured by Silvestri. Locality not indicated but in all probability either Santa Ana in Misiones, Argentina, or Coxipó in Matto Grosso, Brazil.

2. Flight tube obtained at Rio Feio, near

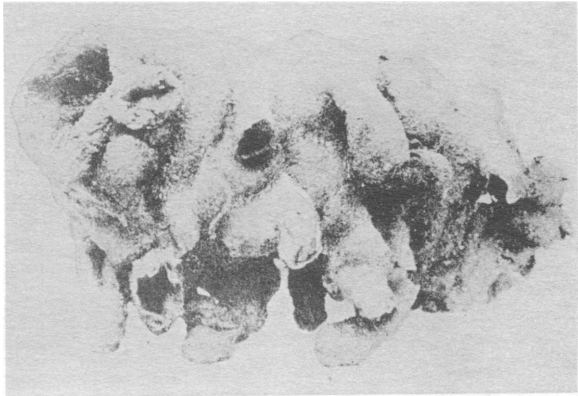
Baurú, in southern Brazil. After H. von Ihering.

3. Flight tube projecting from a nest near the base of a tree on Barro Colorado Island, Canal Zone; length, about 10 inches. Photograph by O. E. Shattuck.

4. Flight tube, 8 inches long, from San Isidro, Costa Rica. The nest to which this flight tube gave entrance was located in the wall of a wooden house. Houses are favored nest sites also of other *Trigona*. Photograph by Anastasio Alfaro.



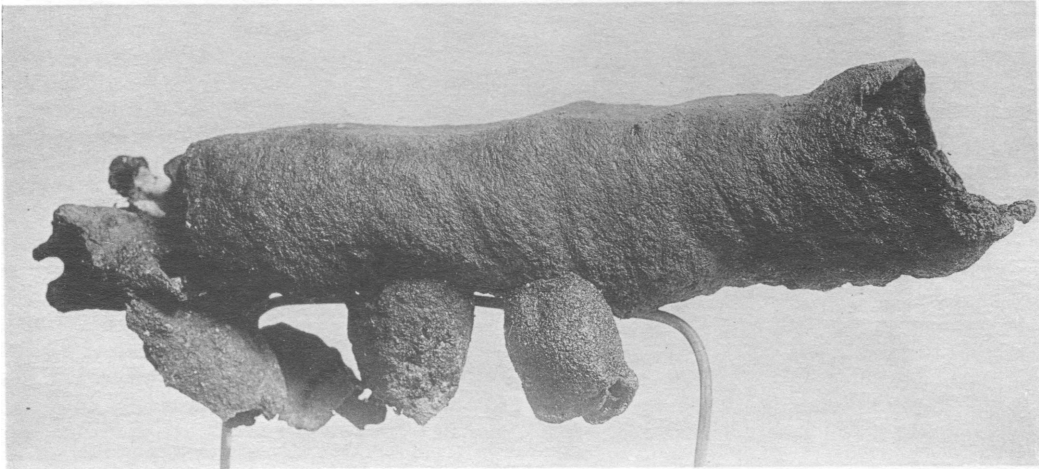
1



2



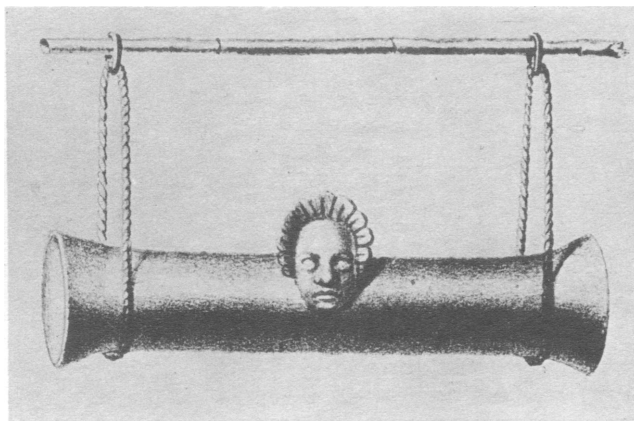
3



4



1



2



3



4

tions that have posed as stingless bees. Thus, H. W. Bates (1870, p. 331) described a cerambycid beetle from the Amazon Valley as *Epimelitta meliponica*, which was captured as it flew about decaying trees. Bates added, "Not distinguishable from a common species of *Melipona* when on the wing."

Wallace (1867, p. 13) had previously alluded to another longicorn beetle, *Charis melipona*, from South America, which "has been so named from its resemblance to a small bee of the genus *Melipona*." Wallace went on to say: "It is one of the most remarkable cases of mimicry, since the beetle has the thorax and body densely hairy like the bee, and the legs are tufted in a manner most unusual in the order Coleoptera."

Certain syrphid flies bear a close resemblance to species of stingless bees. Shannon (1927, p. 17) commented as follows regarding certain syrphids of the genus *Microdon*, subgenus *Ubristes*: "One small group (about ten species) possesses a type of habitus which is so similar to the appearance of the stingless honeybees (*Trigona*) of the American tropics that they may easily be mistaken for them at first sight." *Microdon (Ubristes) lacteipennis* Shannon from the Amazon region is said to be very similar superficially to *Trigona (Trigona) compressa* Latreille, of which *Trigona (Trigona) lacteipennis* Friese is a synonym. *Microdon (Ubristes) goettei* Shan-

non, likewise from the Amazon, owes its specific name to the fact that it is deceptively like *Trigona (Tetragona) goettei* Friese.

ODORS OF STINGLESS BEES

It must be confessed that the paragraphs concerned with odors are placed with diffidence in this section dealing with defense, for it is very easy to conclude that what is disagreeable to the human nostril is also repulsive to the olfactory sense of other organisms, whereas a moment's reflection will convince anyone that this is not the case. To cite only one instance: carrion, nauseous to us, is the *bonne bouche* that attracts other creatures (two-legged, four-legged, and six-legged) from afar owing to its overwhelming stench. It is even possible, therefore, that certain of the unpleasant odors of bees prove a lure rather than a barrier to some of the creatures that are despoilers of bees' nests. Also, as the following text indicates, there are pleasant odors associated with these insects as well as repulsive ones, and the presence of an odor, good or bad, may betray a hive to its enemies. Frankly the discussion of odors is placed here because no better place could be found for it, but the reader is invited to exile it to any other section of this monograph without risking disapproval.

Most stingless bees, Saint-Hilaire concluded (1830, p. 373), have a pleasant odor,

PLATE 4

1. As a rule flight tubes have only a single entrance but sometimes there are two portals of admission, as figured for *Trigona (Tetragona) jaty* F. Smith, a species that ordinarily does not indulge in such duality. After H. von Ihering.

2. Terra-cotta beehive from Tempico, Mexico. In hives of this type were sometimes housed colonies of *Melipona beecheii* E. T. Bennett. In such cases the flight hole was commonly the open mouth of the figure at the center of the hive. The hive was plugged at each side. Periodically the plugs were removed, making the honey pots accessible. After Pierre Huber.

3. Common native hive in use in Mexico and southward is the hollow log, which is plugged at each end as is the terra-cotta hive shown in 2, the plugs, however, being readily removable. A Jicaque Indian of Honduras is here shown in the act of gathering the honey from the honey pots constructed by the bees towards each lateral ex-

tremity of the log. When these pots are pierced, the honey readily flows into the receptacle held to receive it. Photograph by V. W. von Hagen.

4. Maya apiary along the road from Merida to Chichen-Itza. Among the Maya Indians of Yucatan domestication of stingless bees persists to this day, a heritage from a remote past that had its roots in pre-Columbian times. When this photograph was taken (August, 1946) the apiary was in flourishing condition with a total of about 110 nests, each located in a hollow log with a flight hole near the center guarded and completely plugged by a vigilant *Melipona beecheii* E. T. Bennett. The log hives, arranged recedingly along a wooden scaffolding, were piled up on three sides of the structure, and logs scattered about on the ground on the fourth side indicated that at one time that side, too, had had a rampart of hives. Honey is used in a ceremonial drink, balché. Photograph by Dorothy M. Schwarz.

borrowed from the flowers that they visit. The statement is inaccurate, for while some stingless bees are attractive to the human nostril, others are rather revolting, and in either case their reminiscent odors are often unconnected with the flowers they frequent. Thus *Lestrimelitta limão* (F. Smith) owes its specific name to the fact that it gives forth an odor suggestive of lemons, but record is lacking that this bee visits either the fruit or the blossom of the lemon. Indeed, according to H. von Ihering (1886, p. 184), this odor is associated with the fecal matter of these bees. A lemon-like smell is also given forth by *Trigona* (*Nannotrigona*) *testaceicornis* (Lepelletier), according to Ducke (1925, p. 403). Certain other species have an odor like coconuts (Wheeler, 1928, p. 242). Ducke (1925, p. 411) found *Trigona* (*Paratrigona*) *testacea* Klug and varieties of this species pleasant to the nostril, with suggestion of the perfume of roses, but roses do not figure among the floral visits of this species. Even Saint-Hilaire himself noted at least one bee the nest aura of which was not reminiscent of blossoms. He mentioned (1848, p. 93) a very small black bee "of which the odor is that of amber." On his trip along the River of Doubt,¹ Roosevelt (1914, p. 246) encountered small stingless bees "of slightly aromatic odor." So much for pleasant connotations in smells.

In contrast to the instances noted in the previous paragraph are other cases where the odor of the stingless bees is abhorrent. A member of the subgenus *Oxytrigona* was nauseatingly malodorous to Drory (1874, p. 285; 1877, pp. 147-148), while Wheeler (1913, p. 8) compared the stench of yet another *Oxytrigona*, namely, *tataira* variety *mediorufa* Cockerell, to that given forth by the anal glands of dolichoderine ants of the genera *Tapinoma*, *Azteca*, and *Liometopum*, which reminded him of rancid butter. This rancid butter smell also pervaded, according to Wheeler (1913, p. 2), a swarming mass of *Trigona* (*Trigona*) *amalihea* (Olivier) that he roused by thrusting his tweezers into the cluster. Ducke (1925, p. 383) associated a strong and unpleasant resinous smell with

Trigona (*Tetragona*) *heideri* Friese. *Trigona* (*Scaptotrigona*) *bipunctata* (Lepelletier) gives forth, according to H. von Ihering (1903, p. 206), a strong repulsive odor. Hockings (1884, p. 152) noted that the Australian "kootchar" (*Trigona cassiae* Cockerell) when injured or seized between the fingers emits "a not unpleasant, but somewhat ant-like odour," and even ascribed to this odor a defensive function. Hockings claimed that small birds would eat the "karbi," interpreted by him as *Trigona carbonaria* F. Smith, but avoided the "kootchar." A "very strong aromatic odour, something like very rank oil of rose geranium," is credited to the African *Trigona beccarii* Gribodo, when crushed, by Harold Brown (cited by Theobald, 1906, p. 87).

At times the odor of stingless bees (as some of the above records indicate) is powerful, and Jacob (1932, p. 149) made the claim that in the Alto Paraná of Paraguay the natives detect the presence of a hive, which is often well concealed, by the odor it diffuses. Equally acute is the olfactory sense of the Australian black men. Experienced hunters are able to smell their way to the hive of a wild bee, even though it is located at a considerable distance (Basedow, 1925, p. 145). In these cases the possession of an odor is distinctly a breach in the armor of defense rather than a protection against enemies.

The odor within the nest, according to Drory (1872b, p. 174), is somewhat penetrating but not unpleasant; he was basing his remarks on a colony of *Melipona fasciata* variety *scutellaris* Latreille. The odor, in the opinion of Drory, is not that of honey but possibly proceeds from the wax or the droppings of the bees.

In the opening paragraph of this section doubt was expressed as to whether the odor of the bees was really a protective device for keeping enemies at a distance or discouraging their voracity. It seems fitting in conclusion to allude to at least one observer other than Hockings who emphasized the belief that odor has a defensive role in the life of the stingless bee. Marianno (1910c, p. 8) wrote an article on the natural means of defense of the stingless bees and in it made the affirmation that nearly all *Trigona* emit odoriferous secretions which serve as a safeguard

¹ Subsequently named the Rio Roosevelt, in the states of Matto Grosso and Amazonas, Brazil.

against rival insects in the struggle for life. Among these rivals he listed the honeybee, *Apis mellifera* Linnaeus, although that enemy is of very recent introduction in the New World, and wasps. Marianno expressed the view that the odoriferous secretion is unvaried and unmistakable in the case of each species of bee. Not only did it give protection in his estimation against aggressive insects but also against insectivorous birds, a conclusion independently arrived at, as we have seen, by Hockings (1884, p. 152).

ARCHITECTURAL DEFENSES, GUARDIANSHIP OF THE PORTAL, AND NOCTURNAL ACTIVITIES

We have been considering weapons of defense and of aggression that are the endowment of the individual warrior even though employed often or as a rule in mass attack with other similarly equipped members of the hive rather than singly. But it is not merely by personal combat, with employment of the weapons with which nature has endowed them as individuals, that these insect Amazons try to bar the ineligible from their home site or to keep at a distance those who are potential disturbers of their peace. By architectural devices also these bees seek to preserve the integrity of their community life. The portal of admission to the nest is frequently a large protruding cylinder or trumpet. Girard (1875a, p. 568) believed that such an external prolongation of the entrance "serves to shut out all light from the interior and prevents the introduction of insect enemies," while Benton (1894, pp. 18-24) laid emphasis on the exclusively defensive nature of this structure. When the protruding flight tube is large, its inner surface is apt to be thickly studded with guarding bees. In other instances the portal of admission is small and without architectural distinction, and sometimes it is so small that the head of a single watchful portress is sufficient to fill the orifice and exclude unwanted strangers. Such a portress was reported with some misgiving by E. T. Bennett (1831, p. 364) as being on duty for 24 hours, but the statement, derived from notes of Beechey, was based on hearsay, and Huber (1839, p. 22) early expressed doubt as to its accuracy. The bee to which was attributed such constancy in vigil was

Melipona beecheii variety *beecheii* Bennett, but in the case of the closely related *beecheii* variety *fulvipes* Guérin it was the impression of Hill that the sentinel bee was "every now and then relieved" of her guard (cited by Gosse, 1851, p. 467).

Peckolt (1894, p. 89), who in the case of another species [what he interpreted as *Trigona bipunctata* (Lepeletier)] attempted to mark the portress so that he might ascertain how long she maintained vigil, succeeded only in causing her to retreat. When vigil was resumed, it was another bee, not the marked one, that took station. According to Girard (1879, p. 718), in the case of *Melipona fasciata* variety *scutellaris* Latreille, the same sentinel does not remain long on duty. Flying forth to forage, it is immediately replaced by another bee of the hive. On the other hand, in hours of repose, the sentinel guards her post for a long time (pl. 5, fig. 2). Observations of Peckolt indicated that, on moonlit nights at least (and possibly also on other nights), a guard was stationed within the nest entrance even after the portal was closed (1894, pp. 87-91). In contrast to such evidences of foresight, Michener (1946, p. 184) commented on a nest of *Melipona favosa* variety *phenax* Cockerell which, examined after dark, was open and seemingly unguarded.

Defense of the portal would seem the logical explanation of the presence of a portress, yet it is perhaps in order to mention that a different theory as to the functions of this individual obtains among the Popoluca Indians of Vera Cruz, Mexico, who hold that it is the duty of the watchman to prevent the entrance of any bee that does not bear pollen (Foster, 1942, p. 540). It is hardly necessary, in order to dispose of this rather moralistic belief, to mention that pollen is only one of a number of desiderata that returning bees bring to the nest (see pp. 101-111).

At night, the entrance to the nest is sometimes sealed up, another safeguard against visits from those who do not belong to the community, but the barrier to admission is apt to be more or less porous, especially, according to Drory (1874, p. 284), if the night be warm. What are the factors in the environment that prompt the bees to close the

nest and again after a lapse of time to reopen it? Lutz (1931, pp. 5-9), who gave study to this problem in connection with a nest of *Trigona* (*Plebeia*) *mosquito* variety *domiciliorum* Schwarz on Barro Colorado Island, Canal Zone, came to the conclusion that light is an important factor in determining both the opening of the nest and the first flight from it, but withheld opinion whether the factor is the absolute intensity of the light or merely the light's relative intensity. In the case of this particular bee the portal to the nest was not closed normally until after sundown but Lutz, by placing a cone of black paper over the orifice, was able to induce the bees to seal their nest during the early afternoon and in turn to open it when the cone was removed. Of nine "first flights" that he definitely recorded under normal conditions, those on November 23, 24, 27, and December 4 were between 9 and 9:30 A.M., while those on November 28 and 30 and on December 1 and 2 took place between 10:30 and 10:45 A.M.

On the bases of these records *mosquito* variety *domiciliorum* would seem to be a somewhat "late riser" if we use the term "late riser" as the equivalent of late emergence daily from the nest. Its hours for setting forth bear a rough resemblance to those of *Trigona schrottkyi* Friese, the nest entrance of which, according to H. von Ihering (1903, pp. 231-232), "still remained closed between 8 and 10 A.M. notwithstanding the fine weather." Upon *schrottkyi* has been conferred in southern Brazil the popular name of "preguiça," or "lazy bones," although there is uncertainty whether this term of reproach is bestowed because of the tardy appearance of the bee or because of the scant amount of honey that it produces.

Parenthetically, it may be said, in yet another respect there is resemblance between the habits of *mosquito* variety *domiciliorum*, and *schrottkyi* for the nest entrance seems to be more or less alike in the two forms. *Trigona mosquito* variety *domiciliorum* makes "a somewhat dome-shaped oval cover, chiefly of wax" above the slit that gives admission to its nest, and at night closes the portal "by continuing the waxen cover directly across it" (Lutz, 1931, p. 5); *Trigona schrottkyi* Friese closes its entrance hole by

means of "an arched cover of wax" (von Ihering, 1903, p. 231).

Lutz's impression, derived from watching *mosquito* variety *domiciliorum*, was that the bees in starting the day's activities behave as though they are a "combination of an alarm clock and a photometer." The "alarm clock," he goes on to explain, "is a rather mysterious physiological rhythm similar to that with which we are familiar if we tend to awaken at the same time each morning, no matter where we are. The physiological rhythm under discussion here seems to be modified by variations in light. In the case of the bees one may expect the important part of the light to be the ultraviolet."

A witness myself of the experiments of Lutz on *mosquito* variety *domiciliorum*, I am impressed with the accuracy of his observations and the soundness of his conclusions. Yet it is only fair to state that L. E. Cheesman (1933, p. 57) in the case of another species of stingless bees came to the conclusion that temperature was a factor in stirring the foraging activities of the nest occupants. During the night "the temperature of their cage used to go down" and "until it had risen again to 72° not a bee would come out of the nest," stated Cheesman, and again "when the thermometer registered 72°, out they would fly to the flowers." Her observations were continued for more than a year, and during all this time, with one insignificant exception, the correlation of temperature and activity was maintained. Notwithstanding the constancy of this occurrence, it seems to me open to question whether in their native environment the same factor would be operative. It must be remembered that this was an introduced species living under artificial conditions and that a temperature of 72° would be low for the tropics, the natural home of the bees. There it would not be a question of the temperature's rising as high as 72° but falling as low as 72°. In passing, too, it should be mentioned that Drory (1877, pp. 148-149) observed stingless bees flying forth from a nest established in France when the temperature was as low as 18° C.

In contrast to the retarded activities afield of *mosquito* variety *domiciliorum* and of *schrottkyi*, other species give evidence of being much earlier risers. Peckolt (1894, pp.

88-89), who "kept tabs" on the working hours of various species of stingless bees, noted that in some instances the nest was opened to the outer world as early as 5:30 to 6 A.M. Lutz set forth every morning from the Barro Colorado Laboratory well before 6 A.M. to make his studies of the start of the daily activity of a wren (*Troglodytes musculus*), and every day in the darkness of that early morning trudge he was attacked (as I had opportunity to experience on the mornings I accompanied him) by a small swarm of stingless bees. It is almost certain that the same species was responsible for these recurrent attacks, although specimens were obtained on only one of the mornings. These proved to be a *Trigona* of the subgenus *Partamona* very closely related to *testacea* variety *cupira* and possibly not separable from it. Even if the issuance of these bees from the nest in the darkness of the pre-dawn is interpreted as owing to exceptional circumstances, namely, the proximity of a potential intruder, there is other proof that these bees begin their outdoor activities early in the day, for on November 27 of the same year (1930) they were noted to the number of 25 or 30 flying excitedly in front of two of the screens of the dining-room of the laboratory at about 7:20 A.M.

Michener (1946, p. 193) is authority for this statement in the case of the *Partamona* just mentioned: "At night the nest entrances are not closed, nor are 'guards' in evidence. However, if the nest is disturbed, bees will swarm out and attack as in the daytime." Evidently Michener had similar nocturnal experiences to those shared by Lutz and myself.

According to the observations of Ducke (1901, pp. 28, 64) stingless bees pursue their foraging mostly during the morning, rest during the hot midday hours, and then, in the case of many species at least, make their appearance again towards evening. Especially in the case of what he then interpreted as *Trigona* (*Trigona*) *fuscipennis* Friese [which is a synonym of *amalthaea* (Olivier)] and *Trigona* (*Plebeia*) *goeldiana* Friese, specimens were noted on blossoms when it was almost dusk. Later (1902a, p. 324) Ducke indicated that what he had designated as *fuscipennis* should have been recorded as *cupira* F. Smith,

a member of the subgenus *Partamona*.

While stingless bees are not nocturnal in the sense that bees of the genus *Megalopta* and *Xerophasma* or wasps of the genus *Apoica* are nocturnal, it does happen that occasionally *Trigona* are caught at night. Probably these are individuals whose return to the nest was belated. Indeed, in the case of a nest of the Old World *Trigona* (*Tetragona*) *iridipennis* F. Smith observed by Jacobson, bees that arrived too late to gain admission to the nest were frequently noted at night on the walls of the room (Friese, 1914a, p. 56). But it is also possible that now and then such nocturnal meliponids are individuals that have ventured forth after dark from a home community not shut off completely during the hours of darkness from contact with the outside world. Indeed, according to Peckolt (1894, p. 224), *Trigona* (*Trigona*) *ruficrus* (Latreille) does not close its nest at night, and Michener (1946, p. 185) stated that *Trigona testaceicornis* variety *perilampoides* Cresson was the only one of several species of stingless bees studied by him that took the precaution of closing its nest at night.

On the night of November 25, I collected at light bees of the very variety of the subgenus *Partamona* that had attacked Lutz on his pre-dawn walks. Other New World *Trigona* species collected at night include: *amalthaea*, *recurva*, *williana*, *dallatorreana*, and *fulviventrifera* variety *guianae* (all members of the subgenus *Trigona*), and *heideri* (a *Tetragona*). In the Indo-Malayan region there have been collected at light by H. M. Pendlebury and C. B. Kloss such stingless bee species as *thoracica*, *moorei*, *fusco-balteata*, *iridipennis*, and *geissleri* (Schwarz, 1939c, pp. 90, 105, 106, 107, 112, 117). On Papua, near the junction of the Black River with the Palmer River, G. H. H. Tate of the Archbold expedition of 1936-1937 collected by light on June 17, 1936, three workers of *Trigona* (*Tetragona*) *planifrons* F. Smith.

Although, notwithstanding these records, activities outside the nest are usually suspended at night, they may well continue, at least to some extent, within the nest. In the case of a species observed by Peckolt (1893, pp. 580-581), which opened its nest entrance about 6 A.M. on fine days, flew forth in

numbers around 7:30 A.M., and was active in the field till 5:30 P.M., there was evidence that, at least on nights of full moon, some nocturnal duties were being discharged. Thus making visits every half hour to the nest on such nights, Peckolt always found some bees keeping vigil. He was able to observe them thanks to the fact that the barrier to admission of the nest is sieve-like rather than solid. On such nights he made various perforations in the nest entrance with a pin, and, although the guarding bees retreated when this occurred, there presently appeared a large number of excited individuals that ran about uneasily in the flight tube. Peckolt withdrew; when he reappeared 10 minutes later, the breach he had made had been repaired. If stingless bees do not continue nest activities or full nest activities during the night, this episode would indicate that they are at least light sleepers. Another species mentioned by Peckolt (1894, p. 89), which he doubtfully referred to *Trigona* (*Tetragona*) *jaty* F. Smith, gave evidence that it was awake by humming audibly, and in yet another nest [referred by Peckolt to *Trigona bipunctata* (Lepeletier)], a portress could be seen guarding the entrance at all hours, during moonlit nights at least.

An interesting case of nocturnal activity on the part of a colony of stingless bees is noted by L. E. Cheesman (1933, p. 58), who observed the insects engaged in reconstructing the portal of their nest until "far into the night" and felt warranted in drawing the conclusion that this strenuous overtime service was maintained through the entire night, for early next morning the artisans were observed still in full devotion to their task.

We have seen that some stingless bees close their nest at night while others do not. Another device for making access to the nest somewhat difficult is pointed out by Fiebrig (1908, pp. 375, 380). According to his observations on a colony of *Lestrimelitta limão* (F. Smith), this colony protected the approaches to the nest by laying down numerous little globules of wax, in large part not exceeding a pin head in size, and this barricade served as a kind of tanglefoot to capture and retard ants that are inclined to intrude. Here is an architectural device that possibly

functions in a passive way much as does, in an active way, the calculated besmearing of an intruder recorded some pages earlier. These globules that beset the path of the unwary would seem to bear somewhat the same relationship to the sticky weapon in the grasp and control of the attacking bee that a booby trap bears to a deliberately aimed bomb.

What would seem to be even more effective than the placing of scattered droplets of sticky matter is the laying down of a continuous protective band of fresh resinous matter at the mouth of the entrance tube. Jacobson, according to Friese (1914a, p. 43), recorded such a barrier in the case of the Indo-Malayan *Trigona* (*Tetragona*) *iridipennis* F. Smith (Schulz, 1907, pp. 65-73 designated the bee *T. laeviceps* F. Smith in error). Friese (1914a, pp. 43, 46-47, 48, 49), in addition to quoting Jacobson's observations, cited further instances of the establishment of a protective ring of soft sticky resin around the outer rim of the flight tube. Hockings (1884, p. 153) noted a similar barrier in the nest of the Australian "koot-char" (*Trigona cassiae* Cockerell) and, in a subsequent statement quoted by Cockerell (1929a, p. 301), Hockings affirmed that *Trigona carbonaria* F. Smith likewise surrounds the entrance to the nest with a sticky resinous substance. It seems likely that in the case of many another species, too, whenever the flight tube is extended outward, the new resinous addition tends before it hardens to discourage wingless insects like the worker ants from attempting to cross what to them would be an untraversable belt.

Indeed as proof of the effectiveness of this barrier one needs only to cite the observation of Jacobson (Schulz, 1907, pp. 67-68; Friese, 1914a, pp. 47-48), who found glued to this sticky rim of the nest entrance the remains of several ants, *Ecophylla smaragdina* (Fabricius). Furthermore Benton (1894, p. 21), in commenting on nests of *Trigona* observed in the island of Ceylon, told of one nest in the jungle near Kaltura that was located in a small stub. This stub housed, a little farther down, also a colony of ants. The ants, "usually so ravenous and destructive in this as well as other tropical regions," never ventured to cross the sticky tube at the orifice of

the *Trigona* nest. The green tree ants of the genus *Ecophylla* are known for their aggressiveness. Froggatt (1907, p. 119) stated that stingless bees often are captured by these ants, but that the waxy substance of which the nest spouts of the bees are made probably gives protection against the enemy.

Within the nest, the entrance tube leads to the brood chamber, surrounded by its involucrum, instead of to the honey jars, the remote location of which is an additional safeguard from pillage by insects that find honey attractive (Drory, 1873d, p. 70).

LARGE-SCALE WARFARE WITH INSECT ENEMIES

We have seen that in many ways the nest is well designed to give protection to its inmates. It is fortress as well as home. There is the sticky barrier rimming the flight hole, and this serves somewhat the same function and is possibly as effective as was the moat of the medieval castle. There are the watchful guards ready to defend the entrance if the enemy tries to force admission. At night the entrance is frequently sealed, the equivalent in a way of the lifting of the drawbridge. The brood chamber is approached through a narrow tube, which because of its very narrowness is the more easily defended, and in all but nests of the cluster type the brood chamber is enclosed by a protective envelope of usually labyrinthine complexity. The provision containers are securely distant and necessitate a deep penetration of the nest if the enemy that is attracted by honey or pollen wants to taste of their contents. It would seem almost as though these safeguards against invasion precluded the possibility of successful attack. Yet in spite of everything, colonies of stingless bees do not as a rule lead a tranquil existence. As colonies they are threatened especially by other colonial insects of their own hymenopterous order—bees, ants, and wasps.

Almost, one would say, the degree of hostility evidences itself in that sequence, with the bees occupying first place as enemies. In perusing the literature it seems to me I have come upon more instances of internecine warfare between one colony of stingless bees and another than between colonies of these bees and more remotely related groups. Yet

it is to be remembered that many of the observations are based on colonies in domestication and that under the more crowded or compact conditions involved in domestication there is apt to be greater provocation as well as greater opportunity for attack than in the usually more complete isolation under natural conditions in the forest.

L. J. Brunet, who in the seventies of the last century had many species in domestication in Bahia, Brazil, is cited by Raveret-Wattel (1875, p. 753) to the effect that the Meliponidae have as their chief enemies their own kind and that, if a hive of "urucús" (*Melipona fasciata* variety *scutellaris* Latreille) be placed near another hive of the same species that has been there for some time, almost always a combat quickly ensues, especially if the two hives are populous. It is, stated Brunet, a struggle of body against body which terminates ordinarily only through lack of additional available combatants, or, in other words, when the smaller of the two populations engaged is near the point of exhaustion. The mortality on both sides Brunet believed to be about equal. In one of the combats observed, he was able to evaluate the casualties at more than 3000. Yet once the fight was over, Brunet found that gradually the contesting colonies recovered their losses and thereafter usually lived in harmony.

In addition to warring against its own species, *scutellaris* is not averse to measuring its strength against other members of the Meliponidae. Brunet himself noted a combat between this species and what he interpreted as *Trigona* (*Scaptotrigona*) *postica* Latreille. Girard (1875a, p. 572; 1879, p. 712) recorded a combat between *scutellaris* and the much smaller *Melipona marginata* Lepeletier as reported by Drory.

Other combats mentioned by Girard on the authority of Drory were between "*dorsalis*" and *tataira* variety *flaveola* Friese of the "fire defecating" subgenus *Oxytrigona*, and between "*dorsalis*" and *Trigona* (*Tetragona*) *angustula* Latreille. The "*dorsalis*" mentioned by Girard is probably not the true *dorsalis* F. Smith but a form close to *postica*, and the same interpretation is presumably to be applied to the "*dorsalis*" mentioned by H. von Ihering (1903, p. 261). We shall hear

more regarding this combative bee presently.

Warfare between stingless bees may sometimes be inspired by propinquity, but in other cases robbery is the motive. Indeed, in some instances the militant action on the part of one colony against another may extend beyond robbery to the complete occupation by the victorious colony of the nest of the vanquished colony.

It is *Lestrimelitta limão* (F. Smith) in particular that bears an evil reputation as an aggressor. Some writers (F. Müller, 1874b, p. 103; Friese, 1931, pp. 3, 6-10) have gone so far as to assert that it lives solely by robbery. However, this conclusion is probably too sweeping as there seems to be good evidence that, when there is no one to rob, *limão* is capable of pursuing a self-sustaining existence.¹

More than one observer has made note that, on occasions at least, when *limão* has exterminated or evicted the rightful owners of a nest, it takes permanent possession not only of the stores but of the nest itself, which it thereupon proceeds to occupy (F. Müller, 1874b, p. 103; Friese, 1931, pp. 3, 6-10). However, this habit is not confined to *limão*. The bee that H. von Ihering spoke of as "*dorsalis*" but that was probably close to *postica* was accused by that author (1903, p. 261) of completely evicting the conquered colony and establishing itself in the devastated nest hollow, from which it removed the evidences of previous occupation before building its own combs and provision containers.

It is of interest to note that H. von Ihering mentioned, as did Girard, among the victims of this bee a member of the subgenus *Oxytrigona*. Although the aggressive "*dorsalis*" or *postica* does not, as we have seen, confine its attacks to any one subgenus of the stingless bees, the duplication of instances where *Oxytrigona* is involved in combat with "*dorsalis*" would indicate that the fiery fluid of *Oxytrigona* is no effective deterrent to the martial enterprise of "*dorsalis*."

Other species that H. von Ihering rated as particularly predatory were *Melipona fasciata* variety *rufiventris* Lepeletier and *Tri-*

gona (*Trigona*) *ruficrus* (Latreille). Nevertheless, individual members of the former species that tried to enter a hive of *Melipona quadrifasciata* variety *anthidioides* Lepeletier paid for their persistence with their lives (H. von Ihering, 1903, p. 204).

The David and Goliath disproportion of size and strength is recapitulated in at least one of the stingless bees when in combat with its larger adversaries. The tiny *Trigona* (*Tetragona*) *jaty* F. Smith, a mere midget compared with some of the more robust species of Meliponidae, is nevertheless a deceptively formidable adversary. Bertoni (1911, p. 139) went so far as to say that in battles waged to the death between different species of stingless bees it is *jaty* that is always the victor. This estimation of the combative power of *jaty* is partly confirmed by an observation communicated to me by W. Weyrauch. The reader has noted the savage reputation borne by *Lestrimelitta limão* (F. Smith). Yet that bee was, according to Weyrauch, attacked, and successfully attacked, by the dwarf *jaty*.

Thieving need not involve penetration of the nest. There are sneak thieves and pick-pockets of the bee world as well as the housebreakers. An amusing incident is told by Drory (1877, p. 146). On one occasion a number of *Melipona* were occupied in gnawing off propolis and attaching the large lumps of this material to their hind tibiae. Latecomers found it easier to gather these lumps from their fellows than to break off bits from the original quarry. So preoccupied were those who were being robbed that for some time at least they were unaware that they were being defrauded of the fruits of their labor. Here it seems to have been a case of sister robbing sister for the communal good, which is warning that we must refrain from applying moral standards where moral standards are inapplicable.

A strange case is recorded by Hockings (1884, p. 151) involving two swarms of the Australian *Trigona carbonaria* F. Smith that simultaneously set forth from their respective parental hives and met in combat over a box that each group had seemingly selected as its nest site.

Honeybees, owing to man's agency in distributing them throughout the world, have

¹ For a fuller presentation of this subject the reader is referred to the discussion of *Lestrimelitta*, page 176.

become neighbors of the stingless bees in many regions, but neighbors only in the sense of propinquity, not of amity. In a paper presented before the Entomological Society of Washington, Benton (1894, p. 22) told of attempts by both the Cyprian and Palestine varieties of *Apis mellifera* to enter colonies of *Trigona* in Java. In the discussion that followed Mr. E. A. Schwarz referred to a published statement by H. von Ihering "that the native bees had been almost driven out and destroyed in the province of Rio Grande do Sul, Brazil, by *Apis mellifica* (= *mellifera*), which had rapidly spread over the entire district." Bertoni (1911, p. 145) noted that the European honeybee, introduced in Asunción, Paraguay, had gone wild and invaded nearly all the forests. In 1906 it arrived at Puerto Bertoni, Paraguay, crossing 60 leagues of forest in doing so. Competition with so successful a rival can be no easy task for the stingless bees of the region.

In Australia as long ago at least as 1875 escaping swarms of *Apis* had established nests in the forest and in certain regions, it was said, were contributing little by little to the disappearance of the native stingless bees through their attacks (Raveret-Wattel, 1875, p. 758). Such stray swarms of the honeybee, Girard noted (1878, p. 274), would often establish their nest close to that of a species of *Trigona*, sometimes in the very same tree hollow, with merely a partition separating one nest from the other. When one of the two colonies suffered a scarcity of cells, it did not fail to help itself to material in the neighboring colony and immediately a combat ensued that ordinarily ended only with the complete destruction of one or the other of the two battling populations. However, Girard was of the opinion that the little black *Trigona* of Australia did not always fight "at too great a disadvantage with the large bee of Europe." Rayment, writing about a half century later (1932a, p. 247), recorded that thieving honeybees frequently tried to molest the Australian *Trigona* that he had under observation.

The stingless bees are not wholly overawed by the more formidably armed *Apis* and on occasions at least they have demonstrated that they can cope successfully with these aggressors. Drory (1873c, p. 175) and

Raveret-Wattel (1875, pp. 739-744) noted that in combats between *Apis mellifera* Linnaeus and *Melipona fasciata* variety *scutellaris* Latreille it is the former that is usually defeated. Drory frequently found 30 or 40 dead *Apis* before a hive of *scutellaris*, but never a dead *scutellaris*. Taschenberg, too, offered evidence that *scutellaris* can hold its own with something to spare in its encounters with *Apis*. Thus, according to that author (1877, p. 218) at a gathering of German and Austrian beekeepers held in September, 1874, at Halle, Drory displayed a box containing a hive of *scutellaris*. As the day was a mild one for the season, the stingless bees issued forth and mingled with the numerous hive bees. "It was then repeatedly observed," Taschenberg went on to say, "that certain of the domestic bees were bitten to death in flight by the newcomers." In Cuba, according to A. I. Root (1903a, p. 109; 1903b, p. 116) there is a stingless bee [undoubtedly *Melipona beecheii* variety *fulvipes* Guérin] that is so combative that "woe betide the insect of any sort that presumes to come near the sentinel that always guards the doorway day and night. Should a robber Italian presume to come near, a dozen dart for her with lightning rapidity and fury."

The *Melipona* just mentioned (*scutellaris* and *fulvipes*) are relatively large, but colonies of stingless bees made up of small individuals sometimes resist *Apis* with success. We have already noted the combative superiority of *Trigona* (*Tetragona*) *jaty* F. Smith when confronted by other stingless bees. But it also faces *Apis* with courage and persistence. H. Müller (1875b, pp. 50-55) told of a depleted colony of *jaty* that resented the approach of some honeybees bent on robbing them of the honey that Müller had set out for their sustenance. The tiny defenders, ridiculously small compared to the large honeybees, flew at the aggressors, biting into their wings, so that as a rule two Lilliputians clung with mandibles embedded to the fore margin of each anterior wing and rode about in this position as the honeybees scurried here and there trying to get rid of them.

In view of the usual hostility shown by a given bee colony for the members of another bee colony and in view, furthermore, of the instance just recorded in which individuals

of *jaty* attacked with energy intruding honeybees, it is puzzling to learn from van Emelen (1918, pp. 145-150) of a possible case of symbiosis between *jaty* and the honeybee. Yet for seven months a colony of each of these bees lived in amity with the other! Then something occurred that eliminated *jaty* from the scene.

Combativeness in stingless bees manifests itself principally in nest attack and nest defense. But it is not limited to these objectives. On Barro Colorado Island, Canal Zone, a curious combat was witnessed (Schwarz, 1932b, pp. 552-553). A small agitated swarm of insects was milling about in the air only a few feet above the ground. The action was suggestive of the mating flights of certain bembecine wasps, an impression strengthened by the fact that every now and then a pair would drop to earth beneath the dancing swarm. However, the behavior of the insects was inspired by Mars rather than by Venus. All of those taken in pairs were workers of *Trigona* (*Trigona*) *pallida* variety *pallida* (Latreille). In almost all cases they were facing each other, gripping tightly with interlocked mandibles or tumbling over each other like two wrestlers, head to head and body to body. So unrelaxing was their hold that they failed to separate even when they were placed in the killing bottle, and in death each still held the adversary gripped with its mandibles.

Little by little the intense agitation subsided and the surviving Amazons turned their attentions to what had presumably engaged them before the combat. They entered gradually one by one under a large inverted wooden box that concealed a gasoline engine. The box had a small opening below, and through this the bees crawled or flew, but their action showed great timidity. They would approach the entrance only to retreat swiftly, then again muster courage to advance. Their behavior suggested that whatever it was that had so agitated them and prompted them to engage in sororicidal combat had its origin within the mysterious darkness of that box.

An examination of the combatants collected showed that in certain cases several parts of the body, including sometimes the wings, were smeared over and darkened, and presumably these bees had been engaged

just before the fracas in gathering gasoline or grease from the engine, which is a common practice of this species.

At this point it seems in order to mention an observation made near Chichen-Itza on a recent trip to Yucatan. Under a venerable tree that the Maya Indians refer to as "pich" I noted a number of stingless bees separated into two heaps by the root system of the arboreal giant, which some of the natives with whom I spoke asserted to be two centuries old. The bees were for the most part dead or moribund. Over the prostrate ones crawled a few of their fellows, but even these acted sluggishly. Occasionally such an individual would still reveal some slight show of combativeness, seizing and dragging for a short distance one of the inert ones but rarely persisting in these feeble activities and never showing an inclination to fly. Without doubt there had been a major combat with high mortality. The number of specimens that had succumbed locked together in combat, mandible in many instances clashing with mandible, gave evidence that death had not been of the quiescent type. But what did it all mean? The bees, subsequent examination showed, were all workers of *Lestrimelitta limão* (F. Smith). Had two colonies of this pugnacious insect fought in mutual destruction? Had the stingless bee that of all stingless bees is branded as the robber *par excellence* set out to victimize its own kind? Looking searchingly upward into the tree, I could see no evidence anywhere of a *Lestrimelitta* nest; and certainly, if any stingless bee advertises its presence by a conspicuous nest entrance, it is to *Lestrimelitta* that this distinction belongs. Far up in the branches but well to one side of the two piles of dead and dying combatants, there was evidence of a tubular entrance to a *Trigona* nest—what species I could not say. There were, furthermore, some insects, presumably bees, flying in some agitation before the nest but without entering it. Possibly here was the citadel of attack. But, if so, why did the disabled foe reach the earth at a point well removed from the aerial scene of combat instead of falling perpendicularly? More mysterious still, by what miracle did those attacked fail to contribute to the total casualties by so much as a single slain warrior? All of the dead and the

dying were of the master race. In the case of the bees observed one is inclined to think, in the absence of any nest site of *Lestrimelitta* on the tree in question, that probably an army of this genus set forth bent on robbery, but that some untoward incident, some mishap or irritation profoundly disturbing to the temperament of the bees, prompted them to engage in sororicidal strife instead of uniting in a joint act of pillage.

There are numerous allusions to the invasion or attempted invasion of meliponid nests by ants. Indeed, it is the inclination of some to give first place to the ants (in preference to bees) as the outstanding enemies of the Meliponidae. If any weak chink is found in the defenses of the bees' nest, the ants press through the breach and take possession. Black ants, according to E. T. Bennett (1831, p. 365) "sometimes in small, and occasionally in large, bands," engage in desperate struggles with the species he described as *Melipona beecheii*. A variety (*fulvipes*) of this species nesting in a calabash tree (*Crescentia cujete*) in Jamaica was tracked down by a species of arboreal ants that gathered about the entrance to the nest, watching for an opportunity to force admission, but in this instance the vigilance of the portress and other guarding bees stationed nearby prevented the ants from gaining access (Gosse, 1851, p. 467; Wood, 1874, p. 525).

Fiebrig (1908, p. 375) has told of the increasing encroachments upon, and the beleaguering of, a colony of the dreaded *Lestrimelitta limão* (F. Smith) by a voracious colony of *Camponotus*. One morning the demolition of the bee colony had been accomplished. The enemy had found entry seemingly during the night and had wrought its devastation among the brood. In the flight tube were the dead bodies of bees with only an inconsiderable number of slain ants interspersed.

A nest of the subgenus *Partamona* that had been wrapped by Rau (1933, p. 29) in newspaper was found to be occupied three days later by a thriving colony of *Paratrechina longicornis* (Latreille). The ants were established among the cells and, when disturbed, hastily bore off their pupae, which were numbered in the hundreds.

Nests of stingless bees damaged by man

are, of course, particularly vulnerable. Wheeler (1913, p. 7) observed columns of the large leaf-cutting ant [*Atta cephalotes* (Linnaeus)] and of the fire ant [*Solenopsis geminata* (Fabricius)] completing the devastation of a ravaged *Trigona* nest by lapping up the remnants of honey and bearing off in little lumps the softer and sweeter parts of the cerumen, while the defenseless bees tried in spite of all of these discouragements to repair their violated abode.

Against the ever-present threat of ants Brunet was accustomed to protect colonies of stingless bees that he had in transport by plugging the nest entrance at night. When he failed to take such precautions, he sometimes lost the colony because of these rapacious invaders. One species of ant in particular, known locally in Bahia, Brazil, as "tayocas" (*Camponotus atriceps* F. Smith) even struggled across the barrier of water by which Brunet sought to isolate his bees from such unfriendly visitors (cited by Raveret-Wattel, 1875, p. 752; Girard, 1879, p. 712).

According to Peckolt (1894, p. 88), *Trigona* (*Plebeia*) *mosquito* F. Smith is victimized by *Cryptocerus elongatus* (= *Cryptocerus pusillus* Klug), which is known in Brazil as the honey ant. It storms the bees' nest, kills the occupants, consumes the honey, and establishes itself in the tree hollow until another large-scale robbery is undertaken.

One cannot help feeling that the account given by Drory (1888, pp. 27-28) of a devastating attack by termites on a colony of stingless bees in Ceylon involves an error of determination, so out of accord does the account seem with the habits of the Isoptera. However, I give a translation of the passage for such value as it may have: "During three days the bees flew joyously in and out and in the evening I would drop honey to them through the perforations in the roof of their cardboard dwelling. On the fourth day early in the morning, as always, my first trip was to them in order to note how they fly, but none flew forth. To my dismay I note that the entire paper box is covered with hundreds of thousands of small white ants. I remove the lid and behold a fine state of affairs. Not a single *Trigona* remains alive! Even the young, those just emerged from the cell and still completely pale creatures, had disap-

Far to the north of the Australian region in the Palau Islands, lying about 10° east of the Philippine Island of Mindanao, there is also representation of *Trigona* (Yasumatsu, 1935, p. 94; Schwarz, 1939b, pp. 151–152; Cockerell, 1939a, pp. 61, 62). In the Caroline Islands these bees are known to occur as far eastward as Truk Island, which is roughly in the same longitude as the Bismarck Archipelago, and finally outposts of the Meliponidae have been reported from New Georgia, Guadalcanal, and Binskin Island, of the Solomon group (Cockerell, 1911b, p. 176; 1936d, p. 225). But from about longitude 160° E., which roughly bisects Guadalcanal, one may travel eastward through the great stretches of the Pacific without coming upon further insular representatives of the stingless bees. At any rate, if members of the family Meliponidae exist on any of the specks of land dotting this vast expanse of ocean, they have as yet escaped the net of the collector or the notice of the trained observer.

Not until one reaches the west coast of South America do these bees again reappear, to attain their greatest abundance and variety in the New World. With the exception of Chile they are known with certainty from all the countries of South America, although in Argentina they would seem to be confined to the more northern half of that state. One is considerably puzzled regarding their alleged presence in Chile. Herbst (1921, p. 102) stated emphatically that they do not occur there, rejecting the claim of their presence made by Gribodo (1895, p. 201) as fallacious. My own inclination has been to accept the interpretation of Herbst, for I have never come upon stingless bees among Hymenoptera forwarded from Chile. However, it is a little bewildering to encounter the following statement in the narrative of the seventeenth century missionary Vázquez de Espinosa (1942, p. 737). In speaking of the city of Castro, "the last in the kingdom of Chile before the Straits" and "built on the largest island in the Chiloe Archipelago, at 43° S.", the observant friar noted: "All through the woods and forests there are in the trees great numbers of hives of excellent honey, made by the many varieties of bees to be found on those islands." If his observation was authentic, one is almost forced to the conclusion that stingless bees

were numbered among the honey producers of the region. "Many varieties" suggests native bees, not the introduced honeybee of the Old World, and the reference to the nests as arboreal strengthens the impression that the bees belonged to the stingless group. However, there are also wasps that produce honey and, because of this continuity of habit in two different suborders of the Hymenoptera, it is possible that Vázquez de Espinosa interpreted as bees what were, in fact, social wasps.

From South America the meliponid fauna extends northward throughout Central America into Mexico, and a few forms have established themselves in certain of the West Indian islands, especially those not too remote from the continental land masses like Trinidad and Tobago, while in such islands of the Leeward group as Dominica, Guadeloupe, and Montserrat, there is still a thinning representation. Cuba and Jamaica have a single species of the family.

It is possible that more intensive entomological exploration of Haiti may reveal the presence of stingless bees there, for, as noted elsewhere in this Introduction, Columbus obtained wax, possibly that of stingless bees, during his sojourn on this picturesque island (Belknap, 1792, p. 118), but no trace of the actual bees has as yet been found. From Puerto Rico, the Virgin Islands, the northern representatives of the Leeward Islands, not to mention the Bahamas, stingless bees are unknown.

The fact that stingless bees are so poorly represented in the insular apifauna of the West Indies may perhaps be explained by their habits, especially if it be assumed that many insects owe their insular dispersal to the agency of hurricanes. Solitary bees thus whirled to another homeland would more readily establish themselves, aided by the fact that all the females are potential layers of eggs, thus assuring a new generation. But in the case of the stingless bees the queen, on whom the colony is dependent for its egg supply, is a homebody, confined, except for one or possibly two occasions in her lifetime, to the interior of the nest.

If a colony were in the act of swarming and were carried as a unit (queen and workers included) to an insular outpost, there would be

attacks of other stingless bees, of ants, and occasionally of wasps and of cockroaches. These attacks are usually attacks en masse and sometimes take on the character of community warfare, with the penetration of the nest as the objective. But the individual stingless bee, too, as it goes about its tasks in the field falls prey to insects and other arthropods that lie in wait for it.

Indeed some stingless bees are taken by watchful enemies almost at their very doorstep. A salticid spider on Barro Colorado Island, Canal Zone, took station outside a nest of *Trigona* (*Plebeia*) *mosquito* variety *domiciliorum* Schwarz and made its leap, sometimes successfully, sometimes not, at the tiny inmates of the nest that were returning from foraging. In making its jump it tethered itself to the starting point and let out a line of silk just long enough to reach its intended prey. It seems likely that a spider that F. Poey (1852, p. 442) noted near a colony of the Cuban *Melipona beecheii* variety *fulvipes* Guérin had predatory intentions. The little variety *domiciliorum* seemed to accept the toll taken by the spider of members of its colony with resignation. In contrast is the attitude of a species that Peckolt (1894, p. 89) doubtfully referred to *Trigona* (*Tetragona*) *jaty* F. Smith. Peckolt several times observed a spider which took position about 2 cm. beyond the earthen walls of the nest entrance. But it was not permitted to camp thus menacingly at the front door. Immediately six to eight bees hurried forth, but before they had made their approach the spider withdrew, only to reappear after an interval and in turn to be driven away in precisely the same manner. Peckolt (1894, pp. 90-91) reported the presence also of a spider near the nest entrance of a species of *Trigona* that he designated "*tubi*," possibly *Trigona* (*Scaptotrigona*) *tubiba* F. Smith. In this instance, too, the spider was repeatedly driven away by the bees, only to return undaunted, often immediately.

In contrast to the behavior of the jumping spiders that regard the stingless bees as a tidbit was that of the orb-weaver *Nephila maculata*. A female of this spider that had spread its web across a jungle trail in Sarawak, Borneo, was offered five specimens of *Trigona* (*Tetragona*) *apicalis* F. Smith

and two specimens of *Trigona* (*Tetragona*) *thoracica* variety *lacteifasciata* Cameron. To make things easy for her, all the specimens were placed in the web. However, they were unwelcome gifts. The specimens of *apicalis* she rejected *in toto*, tossing them out. One of the specimens of *lacteifasciata* was sampled but apparently proved distasteful, whereupon it, too, was thrown out. The second specimen of *lacteifasciata* suffered a similar fate except that there was no preliminary tasting (Shelford, 1907, pp. lxiii-lxiv; Heikertinger, 1919, p. 357).

We have wandered away from the doorstep of the beehive in following the spiders down a jungle trail. Let us return once more to the threshold to view yet another creature that probably had a predatory fondness for the inmates of the hive. A mantid nymph of the genus *Stegmatophora* was observed by Bristowe (1925, p. 478) close to the entrance of a nest of *Trigona* (*Tetragona*) *jaty* F. Smith, and the suspicion was natural that it had a cupboard love for the small bees of that species. Asilid flies are not averse to eating bees, and a North American species, because of this habit, has been given the name of *apivora*. It comes as no surprise, therefore, that stingless bees, too, are set upon by these assassins (Salt, 1929, p. 454). Indeed, Bingham noted *Asilus* flies persistently hovering around the nest entrance of stingless bees, seizing the latter on the wing as they flew forth (cited by Poulton, 1902, p. 336).

Bristowe (1925, p. 479) is authority for the statement that a sphegid wasp, *Trachypus gomesii* Klug, which occurs abundantly near Rio de Janeiro, Brazil, stocks its nest with stingless bees; *Trigona* (*Trigona*) *ruficrus* (Latreille) is seemingly its principal victim, perhaps because of the abundance of that bee in the region.

Rayment (1944, pp. 4-8) came upon an Australian wasp that he interpreted as *Bembex tridentifera* F. Smith. At first he could not detect any prey being brought into the nest, because the tiny victim is carried pressed close to the wasp's thorax, but an examination of the banquet hall revealed the fact that it was well stocked with stingless bees of several different species of *Trigona*: *carbonaria* F. Smith, *carbonaria* variety *angophorae* Cockerell, *hockingsi* Cockerell, *cassiae*

Cockerell, *cincta* variety *percincta* Cockerell, and even an undescribed species. It was the impression of Rayment from an examination of the exoskeletons that escaped being consumed that each of the wasp larvae devoured "at least a hundred stingless bees."

The frontispiece of the article by Rayment shows a venation for these predatory wasps that, it seems to me, is somewhat at variance with the venation of *Bembex*, and several of the resulting cells of the wing have neither the proportions nor the shape of those of *Bembex*. The specific name Rayment tentatively assigned to this wasp (*tridentifera*) is, accordingly to Dalla Torre (1897, "Catalogus hymenopterorum," vol. 8, p. 511) a synonym of *Bembex palmata* F. Smith.

Ants, having a relish for honey, are a constant menace to stingless bee colonies, but they have also been reported as waylaying individual bees. A colony identified, possibly incorrectly, as *Melipona fasciata* variety *scutellaris* Latreille was received in France in 1861 and put for safekeeping in the greenhouse of the Paris Museum, where, however, the bees were so ceaselessly molested by the ant *Formica* (now *Paratrechina*) *gracilescens* that they had to be removed. Lucas (1862, pp. xxxvii-xxxviii), who reported the incident, stated that the ants not only carried off dead individuals but also living specimens that alighted on plants or on the glass of the conservatory. Twenty-five or 30 ants would attack a single bee, which, at first putting up a valiant defense, ultimately was overcome.

A species of *Megachile* sometimes visited in India a nest of *Trigona* (*Tetragona*) *iridipennis* F. Smith in order to snatch some wax from the entrance (George, 1934, p. 6). Bees of the genus *Megachile* in general build their nests of leaf particles, which they cut with considerable precision for the required purpose. However, a few megachilid bees (especially those belonging to the subgeneric groups *Chelostomoides* Robertson and *Hackeriapis* Cockerell) are resin gatherers, and Rau (1943, p. 644) has recently recorded an instance where *Megachile peruviana* F. Smith appropriated the old paper nests of such social wasps as *Polistes instabilis* and a *Mischocyttarus* species and "by building partitions and plugging the openings of the cells with a resinous substance," converted them into brood cham-

bers for the reception of its young. It is interesting in view of this observation to find an Indian *Megachile* using the nest of another member of the Hymenoptera (a *Trigona*) as a quarry for building material.

ARTHROPOD ENEMIES AND ASSOCIATES WITHIN THE NEST

Salt (1929, pp. 445-470) has done an immeasurable service in assembling and classifying, with illuminating comment, the instances in the literature concerned with insects and other arthropods that have becomeinquilines in the nests of stingless bees. His modest insistence that his contribution is merely of a preliminary nature should not deter anyone from placing the paper high on the list of required reading for those interested in the social insects and more particularly in the social Hymenoptera. The excellence of Salt's paper and its accessibility relieve me of the necessity of giving more than a brief summary of the subject based on his investigation of the facts. Of arthropods found in the nests of stingless bees Salt was able to record no fewer than 10 orders, 19 families, 30 genera, and 37 species. Of the 19 families, at least 17 also include myrmecophiles and at least 13 termitophiles among their number. Of the 30 genera, however, only three are also associated with ants and only four with termites. Not one of the 37 species is either myrmecophilous or termitophilous. From this Salt concluded (p. 463): "It appears, then, that although the associates of stingless bees are derived from the same sources (families) as those of ants and termites, they have developed along entirely independent lines. They are not organisms which first lived with other social insects, ants or termites, and then enlarged their sphere to include the nests of stingless bees, but an entirely new set of forms developed in direct relation with their meliponine hosts." Salt went on to point out how the several special conditions (architectural, dietary, and the like) that obtain in the nests of stingless bees would tend "to influence profoundly the form and habits of the organisms that would dwell among them."

It seemed unlikely to Salt that any of the strangers sharing the nest with Meliponidae could be classed as symphiles or true guests,

although he indicated that a possible exception might be certain Homoptera. The great majority of the meliponophiles are presumably therefore either synoeketes (inquilines that are tolerated) or synechthrans (inquilines that have the ill will of their hosts). Certain tentative explanations as to how the putative synechthrans escape the persecution of the bees are discussed by Salt, and his account closes with comparative figures as to the number of representatives of each order and class of arthropods associated, respectively, with the stingless bees, the ants, and the termites. In the case of each of these three groups of social insects, it is the Coleoptera that greatly outrank all other forms in the number of associates provided.

How completely the form of some of the Coleoptera is adapted to the unfriendly environment in which they are compelled to live is well illustrated in an account that Arrow (1930, pp. 183-184) gave of *Cleido-steihus meliponae*, a beetle found in nests of the African *Trigona alinderi* (Alfken). The entire physical plan of this beetle, according to Arrow, seems to be designed to prevent the bees from finding an accessible biting surface. "The absence of eyes renders the head so small that it can be withdrawn into a kind of pocket, where it is completely concealed. The legs fold up and fit into cavities beneath the expanded margins of the body, and so, when the little creature (it is barely one-sixteenth of an inch long) 'sits tight' with its outer edges pressed close to the surface on which it rests, all its vulnerable parts are enclosed like those of a limpet upon a rock. In addition, the two wing-cases, having no wings to uncover, are firmly fixed together; and there is a whole series of interlocking devices to hold the front and hinder parts of the body rigidly attached, as though to resist any attempt to pull the insect from its base."

One wonders with Arrow how such a creature (sightless, incapable of flight, and with only limited powers of locomotion) gets from one stingless bee nest to another. The life of any one stingless bee colony is at best limited. Yet the species of beetle has not died out. Its degenerate structure, with so many of the organs essential to an active life lacking, indicates, as Arrow pointed out, that the beetle has been devoted to a parasitic existence for a

very great succession of generations. Through all that span of time it has managed to live on in colony after colony of the bees. Yet such colonies are often widely separated from one another and it would seem to be impossible for a creature that cannot fly or see to bridge them unaided. The most plausible theory is that the beetle travels to a new nest site by becoming attached to its host at the time the latter is swarming. But is it as an adult, or as a larva, or possibly even as an egg that the beetle makes its aerial ride to some distant tree where the bees are about to establish their quarters? Arrow seemed to think that it may be as a larva that the journey is made, and finds support for this interpretation in the fact that certain other beetle larvae that live in the nests of solitary bees get transported by clinging to the hairs of their hosts. Very likely this is the case, but it seems in order to indicate that the interesting scavenger beetle *Antherophagus*, which is a common associate in the nests of bumblebees, gets transportation as an adult by clinging to the legs, antennae, or even the tongue of the bee (Plath, 1934, p. 57).

Both the degree to which a colony of stingless bees may become infested with undesirable tenants and the protective measures taken by the bees are well illustrated in an account that Rayment (1932a, pp. 246-247; 1935, pp. 530, 546-548) gave of his Australian *Trigona carbonaria* F. Smith when, after being transported for 90 hours, the bees finally reached their destination and were permitted to resume their activities. Within 10 minutes from the time when communication between the nest and the outer world was reestablished workers were exceedingly preoccupied in carrying out the spiny larvae and the pupae of a small fly. These were borne out at the rate of five every minute during the first day and at the end of 48 hours many thousands of these evicted inquilines were strewn about the hives.

Mention may also be made in this connection of the account that Rau (1933, p. 33) gave of a nest of *Lestrimelitta limão* (F. Smith) on Barro Colorado Island, Canal Zone. On the ground under the nest spout where the bees had dropped particles of refuse from the nest, "the earth for a con-

siderable depth was heaving with the larvae of a Dipterous scavenger, *Hermetia illucens* L." It seems possible that this accumulation of fly larvae may have represented original ejections from the nest.

Also suggesting a purging of the nest is the record submitted by Pagden of specimens of *Trigona* (*Tetragona*) *fimbriata* variety *fimbriata* F. Smith which were carrying creamy white larvae in their mandibles (Schwarz, 1939c, p. 103).

Not always, however, is it the habit to render the immature stages of inquilines helpless by throwing them out bodily. Another method of disposing of them is to seal them down with a covering of wax and resin. Rayment (1932b, p. 39; 1935, p. 547) noted that this treatment was accorded to hundreds of pupae of a fly that infested a colony of *Trigona carbonaria* F. Smith.

Even much larger creatures are sometimes sealed into the nest and thus rendered innocuous. Thus Jacob (1932, p. 152) told of a large beetle of the genus *Phileurus*, 30 mm. long, which had been fastened down, possibly while in the living state, in the nest of a colony of *Trigona* (*Tetragona*) *jaty* F. Smith. All the legs were attached, only the head, abdomen, and a part of one of the hind legs being free.

In addition to the arthropods that share the nest with stingless bees, a word of mention is due also to those organisms that share the person of the bees themselves. Almost nothing is known regarding the diseases of stingless bees. Foul brood, a devastating ailment of the honeybee, seemingly has not extended its ravages to the Meliponidae. Rayment (1932b, p. 42) examined hundreds of *Trigona* cells and the juices of many larval bees but was unable to trace the responsible organism, *Bacillus larvae*. The dipterous parasite, the so-called bee louse *Braula coeca*, with which the honeybee is sometimes plagued, has not been found on the person of the stingless bees. Isle of Wight disease, an ailment of the honeybee caused by the entry of a mite, *Acarapis woodi*, into the tracheal trunks of the thorax, is not known among the stingless bees. But other mites are found on these bees, and sometimes large numbers of bees in a given colony are infested. Thus out of some 400 workers of *Trigona* (*Partamona*)

testacea variety *testacea* (Klug) that I examined from a nest collected by J. C. Bradley in the Colony of the Perené, Peru, nearly 100 were thus infested. The largest number of mites counted on a specimen was three, and for the most part only a single mite was present on a specimen. The mites were of two kinds, or possibly they represented two stages of development: one convex in dorsal aspect, which was in the majority, and the other of flat dorsal aspect. At least the convex form was located, with rare exceptions, on the outer surface of the broad and bowl-like hind tibiae of the bees, in the vast majority of cases on the apical half of the joint and usually close to the edge, sometimes grasping one of the eyelash-like fringing hairs. So partial did these mites seem to be to this area that in several cases where two mites occur on one specimen, the mites had arranged themselves one on each hind tibia in almost precise bilateral symmetry. It has been suggested by Le Veque (1930, Amer. Mus. Novitates, no. 434, p. 1) that those mites that occupy the peculiar "mite pocket" of bees of the genus *Mesotrichia* serve possibly a useful function in devouring stray pollen grains on the bee's body which, if allowed to remain, might be attacked by fungi. Has the presence of the mites of *testacea* on the hind tibiae, where the greatest concentration of pollen is ordinarily to be found, a similar explanation?

In a nest population of 6529 *Trigona* (*Trigona*) *corvina* Cockerell collected by C. D. Michener in Juan Mina, Canal Zone, on April 27, 1945, which I was privileged to examine, many of the workers bore mites of a brownish to reddish color. Again in this case a favorite location of the mite was on the hind tibiae of the bee, often in the depression at the apex of the joint. Many of these bees had their hind tibiae laden with a sticky substance.

Mites, however, do not confine their attentions to the bees themselves. Salt (1929, p. 447) found *Hypoaspis meliponarum* Vitzthum "moving over the nest structures, chiefly in the region of the pollen-pots" of *Melipona interrupta* variety *salti* Schwarz. The same author found mites of the genus *Trigonholaspis* on the comb of *Trigona* (*Trigona*) *amalihea* (Olivier), and in one or two cases he even came upon individuals

within the closed cells of the bees, on one occasion actually attached to the bee pupa "under the thorax apparently to the left middle leg." At least two families of mites, Gamasidae and Laelaptidae, are meliponophilous.

A field note accompanying some specimens of *Lestrimelitta limão* (F. Smith) collected at Arena Forest, Trinidad, British West Indies, February 21, 1945, by E. McC. Callan speaks of "large numbers of gamasid mites in entrance, especially in blind 'fingers' [presumably the stalactite-like formations of the entrance tube.]"

Although stingless bees share their nest with so many diverse organisms, they are, as is the honeybee, free from infestation by inquiline genera of their own family. Nowhere has anything comparable to the relationship that obtains between the guest bee *Psithyrus* and the host bee *Bombus* been discovered in nests of meliponids and, in view of the extensive collecting that has been done, it is highly unlikely that any cuckoo bee exists in their nests. H. Müller at one time (1875b, pp. 49-50) believed that his brother had discovered certain cuckoo meliponids in the nests of two different species of *Melipona* and even proceeded to bestow names upon these finds. But the putative cuckoos proved to be merely the young virgin queens of the hive (F. Müller, 1878, pp. 228-231). One is inclined to suspect, too, that when Schulz (1905c, p. 141) advances the theory [based on observations of callows of *Trigona* (*Partamona*) *testacea* variety *cupira* F. Smith] that structural changes and not merely changes of coloration occur during the progress from the callow condition to the fully adult condition, he may have confused workers with virgin queens. At any rate, the longer malar space, which he ascribes to the callow worker, is a character that, along with others, particularly differentiates the queen from the worker.

A wrong interpretation that under high authority finds its way into the literature is sometimes hard to dislodge, and F. Müller's "cuckoo bees" are doubtless responsible for the statement that appeared and reappeared in the successive editions of Claus' "Elementary text-book of zoology," both in the English (1885, p. 599) and French translations (1889, p. 810) and no doubt also in the

German original (1880), to the effect that in the genus *Melipona*, as in *Bombus*, species occur that construct no nests but lay their eggs in the nests of other species.

VERTEBRATE ENEMIES

Among the vertebrate enemies of the stingless bees certain observers (Saint-Hilaire, 1830, p. 373; Holmberg, 1887, p. 256) have given man the place of preëminence, while others have doubtless refrained from doing so mainly because the fact seemed obvious. Near settlements, man indubitably is the most sinister threat to these bees. In some cases (see section on domestication, p. 143) he has permitted colonies to continue, merely robbing them periodically of the fruits of their labor, but in most instances he has treated wild nests with ruthless disregard of their continuity, destroying nest site as well as brood in his eagerness to gather the plunder of honey and wax. As indicating the extent to which certain areas have been denuded of wild colonies, Schulz (1905c, p. 142) stated that in those forested areas of the Amazon region that adjoin human settlements there are encountered everywhere trees from which an oblong section of the trunk is missing, proof that on an earlier occasion, a stingless bee nest has been laid bare by the ax. According to Wied Neuwied, the Botocudo (1820-1821, p. 34) and the Camacans¹ (pp. 219, 223), both native Indian tribes of Brazil, were industrious gatherers of the products of the bees. The Botocudo, ordinarily not to be budged, would climb the highest trees eagerly and swiftly if a gathering of honey was the objective. The Camacans even domesticated stingless bees but were not conservative of the bees themselves, which were placed with wax in water. The resulting brew was said to be intoxicating.

In the Old World, too, man has proved ruthless in his pursuit of honey. The Kaffirs, according to Marais (1912, pp. 790, 792), destroy enormous quantities of hives each year, but the descendants of the white settlers of the region, too, have become "very clever

¹ I am indebted to Dr. A. Métraux of the Bureau of American Ethnology for informing me that the designation Camacan will be used in the "Handbook of South American Indians" for this people rather than Mongoyó, which is a synonym.

honey-hunters" and have contributed to the destruction. In fact, after berating the African mustelid known as the ratel for its persistent plundering of bee colonies, Marais concluded that: "If, however, the bees could express any opinion, I think they would prefer the nocturnal depredations of the ratel to the marauding of man with so able a coadjutor as the honey-bird." Speaking of northwest Ethiopia, R. E. Cheesman (1936, p. 64) made the statement that "all hollow trees have either a swarm of wild bees or a square hole cut where the adze has enlarged the entrance in order to admit the hand of a honey-gatherer." The fact that Cheesman added somewhat naively that the Abyssinians could "put their hand into the middle of the swarm" and remove the honey "without being stung" is pretty clear indication that the bees were of the stingless kind.

In estimating the destructiveness of man, it must be remembered that there are vast areas man has not penetrated. Even near the trails, in the green confusion of the tropical forest there is many a nest concealed from vision, while beyond, in the pathless stretches, are others far removed from access. Here vertebrates other than man can ravage the nests with little fear of detection, and it is a question whether the unrecorded instances of such destruction on the part of this group of vertebrates or that do not mount up to a total in excess of that ascribable to man, whose ravages are more easily traced.

Among the avian enemies of the stingless bees must be classed unquestionably the woodpecker. On the bark of a tree housing a nest of *Melipona quadrifasciata* variety *anthidioides* Lepeletier were evidences of the attack of a woodpecker, and the man who collected the nest was inclined to believe that these marks represented endeavors on the part of the woodpecker to penetrate to the bee's nest (H. von Ihering, 1903, p. 190). Later in the same work (1903, p. 274) H. von Ihering again alluded to the observations by Brazilian woodsmen of the propensity of woodpeckers to attack nests of stingless bees and then went on to cite two instances from his own experience where the bark in the neighborhood of the flight hole of the stingless bees' nest showed damage by woodpeckers, notwithstanding the fact that this bark was

entirely healthy at this point, so that a search on the part of the woodpecker for larvae living beneath the bark could not be offered in explanation of the attack. As a species especially victimized in Rio Grande do Sul, Brazil, von Ihering mentioned *Trigona (Scaptotrigona) tubiba* F. Smith and went on to say that, if the information as to this species is correct, then the woodpeckers are always assured of food, for a few pecks at the trunk of the tree will produce an outpouring of the bees from the nest in numbers to satisfy even a bird's appetite. Numerous specimens of a species of stingless bee were obtained from the stomach of the woodpecker *Ceophloeus lineatus*, and, as it is customary to name a species after its collector, this bee was described as *Trigona (Hypotrigona) ceophloeae* (Schwarz, 1938, pp. 505-508, pl. 61, upper D). Dent (1886, pp. 89-90) asserted that *Trigona (Tetragona) jaty* F. Smith seals the entrance to its nest with resin "to prevent woodpeckers and other birds getting into the nest." The "carpinteros"—and what avian worker in wood better deserves the name of "carpenter" than the woodpecker?—are accused also by Holmberg (1887, p. 256), and particularly *Dryocopus atriventris*, as the chief culprit of the Picidae. The Picidae, or woodpeckers, are mentioned also by Bertoni (1911, p. 139) as persecutors of the stingless bees whenever the wood is soft enough to be penetrated.

Other bee eating birds, according to H. von Ihering (1903, p. 274) are to be found among the Dendrocolaptidae, which include the tree creepers, and the Galbulidae, or jacamars, and an outstanding ravager, according to this author, is *Dendrocolaptes picumnus*. Less specific than von Ihering is Saint-Hilaire (1830, p. 373), who merely stated that various species of birds are destructive of stingless bees in Brazil. Among such birds Brunet, also writing from Brazil, listed the kingbird and swallows (cited by Raveret-Wattel, 1875, p. 753; and Girard, 1879, p. 712). The ravages of the kingbird among our bees were, however, not confined to Brazil. F. Poey (1852, p. 442), keen student of nature in Cuba, found the kingbird a destructive agent in that area of the world, too, commenting that not without reason has it been named *Tyrannus*. A bird known to the Maya as "Ah-Ya"

(sometimes spelled "i-a"), said to be *Myiarchus yucatanensis* Lawrence, the Yucatan crested flycatcher, is referred to as "a bird which eats bees" (Roys, 1931, p. 342), and very probably Meliponidae are among its victims.

In contrast to these predatory relationships between birds and stingless bees, Myers (1935a, p. 13), who made a study of nesting associations of birds with social insects, found an instance of a meliponid colony in close proximity in the same tree with a small colony of the yellow-backed cassique (*Cacicus cela*). The repeated instances where these birds have made their nests close to those of social Hymenoptera, particularly stinging wasps, have been interpreted as a protective device against marauders, who, although tempted to seize the birds, might be restrained by the presence of a formidable colony of the insects.

Turning to the Old World, several small birds, according to Hockings (1884, p. 155), eat the Australian "karbi" or, as he interprets it, *Trigona carbonaria* F. Smith, but do not molest its compatriot, the "kootchar" (*Trigona cassiae* Cockerell). The honeyeaters, or Meliphagidae, so well represented in Australia, include many that are largely insectivorous or that, at least, take small insects with their honey or nectar. Bees have been mentioned among the victims of some species.

The most interesting avian enemy of bees (whether one considers the Old World or the New) is, however, the African honey guide or honey bird. As Chapin (1924, p. 329) has well said: "Were a facetious journalist to attempt to endow a mythical bird with some startling but imaginary instinct, he would hardly be likely to go to the lengths to which nature has gone in the case of the common honey guide of Africa." This bird, after having located one or more colonies of bees, tries to attract the attention of the passer-by through its persistent chattering and, if it is successful in these efforts, flies ahead of its human follower until it has led him to the honey quarry. Bee comb and bee larvae are the reward of the bird, which needs the interested assistance of man or of some mammal like the honey badger, *Mellivora*, to lay bare these sources of food. So well recognized are the services rendered by the honey guide that,

according to Chapin, it was the practice formerly in the Azande tribe of the north-eastern Congo to cut off the ears of anyone who was so rash and so foolish as to kill one of these valued birds.

Usually, it would seem, the honey guide conducts to colonies of *Apis*, but the nests of stingless bees, too, are presumably sought. Marais (1912, p. 792) referred to two species of stingless Moka bees in the northern Transvaal, one of which lives in very hard and virtually impenetrable ground and has been interpreted as "closely allied to, if not identical with, *Trigona clypeata*, Friese" by C. B. Hardenberg (cited by Marais, 1912, p. 794). This species enjoys protection "against all honey thieves and especially against man and the ratel." The honey guide never leads its collaborators to such a nest, stated Marais, but by implication the more accessible nests of the other species of Moka bee are possible objects of the conducted tours. As Chapin has pointed out (1924, p. 333), only *Apis* and *Trigona* furnish wax, to which the honey guide is partial. Colonies of the latter as well as of the former, would seem, therefore, properly to come within the sphere of interest of the bird. Nevertheless, the honey guide is selective. It avoids not only certain ground nesting bees but also some of the arboreal denizens. According to Hughes (1933, p. 335), the honey birds do not guide you "to the nests of the tiny black bee, which are generally found in the hollow knot of a tree, and easily spotted by the thick black streak trailing down beneath the opening."

Turning now from birds to mammals, in Africa the ratel shows an interest in bee colonies as epicurean as that of the honey guide. In recognition of the partiality of this animal for honey, it has had conferred upon it the generic name *Mellivora*. "Loud and deep," stated Marais (1912, pp. 791-792), "are the execrations of the hunter who has been led a hot and laborious march through kloof and poort by a honey-bird to find the hive ransacked and rifled of every vestige of honey by the ratel." This mustelid is, therefore, according to Marais, next to the makopa "the best hated of animals that haunt the bush veld." The ratel itself is frequently a follower of the honey guide to some quarry of honey.

In Borneo the little Malayan bear (*Helarctos malayanus*) is said to be "a very glutton for honey" (Beccari, 1904, p. 106). Its depredations are committed especially against the honeybee *Apis dorsata* Fabricius, but no doubt an animal so fond of a product of the bees does not forego the opportunity of raiding also the pantries of the indigenous Meliponidae. Indeed, after making this surmise, I came upon an article by Jacobson (1927, p. 121) in which he tells of the havoc wrought by the honey bear in the Netherlands East Indies among colonies not only of *Apis dorsata* and *Apis indica* but also of *Trigona*.

In the New World a predatory visitor is the armadillo. This animal is accused by Saint-Hilaire (1830, p. 373) and by Brunet (cited by Raveret-Wattel, 1875, p. 753; Girard, 1879, p. 712) of destroying stingless bees that nest in the ground. Their Brazilian records of the destructiveness of the armadillo are supplemented by the Argentine record of Homberg (1887, p. 256), who pronounced this mammal destructive of stingless bees in Misiones. It is a far cry from this region to Mexico and yet, while I have not come upon records of the pillaging of meliponid nests by armadillos in the more northern part of the range of these animals, I have been inclined to wonder whether the association in the Mayan Codex Tro-Cortesianus of the armadillo and the bee may not have a natural history basis as well as a mythological significance.

Notable for making miserable the life of stingless bees are the anteaters. A century and a half ago Azara in his wanderings through South America from 1781 to 1801 was aware of the nefarious part these insect eating mammals play in the life of the Meliponidae. It was the arboreal anteater, which he designated "caguaré," a species of the genus *Tamandua*, that Azara (1810, p. 133) accused of climbing the trees, assisted by its prehensile tail, and robbing nests of both honey and bees. This early observation has received full confirmation. Indeed the popular names, "colmeneros" and "meleros," respectively, "bee-keepers" and "honey merchants," have been conferred in South America upon members of the genus *Tamandua* in recognition of their partiality for

honey (Cabrera and Yepes, 1940, pp. 238-240).

Another mammal that is notably fond of honey is *Tayra barbara*, which seeks the wild bee colonies in trees for its depredations. The Brazilian name of this animal is "irara," which is derived from two Guaraní words, "ira," meaning honey, and "nara," signifying master or lord, thus "lord of the honey" (Cabrera and Yepes, 1940, p. 145). The Portuguese designation "papamel" also stamps it as a honey thief (H. von Ihering, 1903, p. 273). "Oso melero," or honey bear, is, Dr. G. H. H. Tate tells me, the name given this animal in Ecuador. "Oso colmenero," or apiarist bear, is the term used in Yucatan; the Mayan equivalent is "zaam hol" (Juan Pió Pérez, 1866-1877, p. 412). In the "Relaciones de Yucatan," a collection of unedited documents relating to the discovery, conquest, and organization of the ancient Spanish possessions overseas, appears (vol. 1, p. 303) the following account of the *Tayra*, which, even if slightly embellished, indicates the evil repute this animal had because it rivaled man in its appreciation of the products of the bee: "There is another animal which they call camhol, which is a bear the size of a dog. They eat nothing but honey, of which there is a large quantity. As people keep hives outside of town, if they neglect them these animals will destroy them."

Hermann von Ihering (1903, p. 274) had once seen a nest at which an "irara" had bitten in his futile attempts to reach the honey; these beasts of prey are able as a rule to get at the nest only if a large enough hollow in the tree enables them to push forward to it. Yet their ravages are often highly effective.

Another animal that through its partiality for honey has acquired a name derived from the word "ira" is the "eyra cat" (*Felis eyra*).

From a description that was supplied, Holmberg (1887, p. 256) suspected that yet another mammalian enemy of the stingless bees is the crab eating raccoon, *Procyon cancrivorus*. Holmberg made efforts to acquire a live specimen of this raccoon, possibly with a view to test its behavior towards the bees, but he was unable to effect a purchase, and the next day the animal was wantonly put to death in order to satisfy a whim of its owner.

Among mammalian enemies of the sting-

less bees Brunet (cited by Raveret-Wattel, 1875, p. 753; and Girard, 1879, p. 712) numbered the kinkajou (*Cercoleptes caudivolvulus*) and the grison (*Galictis grison*).

One night a nest of stingless bees in Costa Rica was destroyed by some prowler. A trap was set above the box housing the colony and at intervals of several hours two immature specimens of the South and Central American house rat, *Rattus alexandrinus*, the presumable culprits, were caught (Alfaro, 1939, pp. 149-150).

An intriguing if rather incredible story of the partiality on the part of mammals for the products of stingless bees is that recorded by the Spanish padre, Joseph Gumilla, who wrote regarding the Orinoco River in 1741. A second edition of his work appeared in 1745 and, thanks to the rare book division of the New York Public Library, I was able to examine a copy of this edition, and to read the entertaining account given by Gumilla. According to that traveler there is a small species of monkey in the Orinoco region that after the manner of saltid spiders and the "lagartiscos," presently to be referred to, takes position in front of the hive and devours the issuing and returning bees "to the last one." This in itself would be an achievement sufficiently remarkable, particularly in the case of a populous colony, but it pales in significance before the further claims that are made. For, according to Gumilla, the devouring of the bees is only the first course of the banquet. The honey secreted in the tree hollow is the next objective. If the honey can be reached by hand, well and good; in such a case the monkey cleans out the hive. But if the hand proves ineffectual and lacks sufficient reach, the monkey still has, as a last resort, his prehensile tail and, according to the amazing account, he is believed to insert it into the hive, permit it to get soaked with honey, and then to withdraw it so as to taste of the caudal load of sweets. This procedure is supposed to go on until the tail has reached all the honey pots that are accessible and all means have been exhausted for obtaining the residue of honey (Gumilla, 1745, pp. 341-342; also cited by Nordenskiöld, 1929a, p. 171).

One dislikes casting doubt upon so delightful a conception. The prehensile tail of the

South American monkeys is doubtless a very adaptable tool, but it takes considerable imagination to believe that it is put to such extreme uses as the one cited. To reach the honey pots the tail would frequently have to make its way through the successive layers of brood comb, not an easy penetration, and the honey pots themselves would have to be smashed before their contents could be mopped up.

It seems likely, however, that monkeys, too, may have recognized the fact that bee colonies provide palatable food, even if the methods they apply to obtain that food are not so fantastic as that propounded by Gumilla. Thus Sharp (1899, p. 62), in referring to the many enemies of stingless bees, stated that they ranged "from man and monkeys downward," while Chapin (1924, p. 334) hazarded "the bold assumption" that in forests of western equatorial Africa where the honey badger *Mellivora* is absent or very rare and hence not readily available as a collaborator, the bird known as the honey guide endeavors to enlist the aid of mammals such as "squirrels, small carnivores, lemurs, or monkeys" in laying bare the treasures of the bee colonies. Furthermore Westwood (1840, p. 286) was of the opinion that certain *Trigona*, such as *amalthaea*, that construct exposed nests place them "at the tops of the branches of trees, out of the reach of monkeys," but his premise that the nests are placed in the most inaccessible part of the tree does not necessarily hold.

The fantastic account of the monkey that uses its tail to extract honey from a bee's nest strains belief to the utmost. Strangely enough, it is not the only instance cited of this curious alleged use of the caudal appendage. The coyote is credited with a similar adaptability according to Storm (1945, p. 348), who cited as her authority Dr. Eduardo Ruiz. Bees referred to as "capáricha," which make their nest in the ground, are sought out by the crafty coyote, who forces his tail into the nest in order to enrage the insects and invite their attack. When the angry bees have gathered in numbers on the tail, the coyote dashes away to a distance, where he shakes off the tenacious enemies. Having thus gotten rid of the guardians of the nest, he returns to enjoy the fruit of his conquest. Again the tail

comes into play, but this time with the object of steeping it in honey as the preliminary to an enjoyable feast.

The scene of these improbable happenings relating to the coyote is the Mexican State of Michoacan. Thus we have two stories that are presumably derived from each other (or more likely from a common source) occurring in territories so widely separated as northern South America and southern Mexico. While these are the only two instances I have been able to find of the alleged use of the tail of animals for the extraction of stingless bee honey, the accounts presumably are linked with similar stories in which the tail is used to extract food other than honey. Edwin Way Teale has kindly called my attention to a recent article by J. D. Ratcliff entitled "Relentless enemy of man" (This Week Mag., February, 12, 1939, p. 5) in which the author refers to the rats as stealing food "by dipping their tails in bottle necks too small for their snouts."

Some mammals, it is true, make expert use of their tails in grasping objects. Both the New World monkeys and the kinkajou swing suspended by their tails from the limbs of trees, and in an article contributed by Edmund Heller (1932, Bull. Washington Park Zool. Soc., vol. 3, nos. 2 and 3, p. 5) the statement is made that, "when really hard pressed," the kinkajou, "uses his prehensile tail as a fifth hand and can grasp any objects he wants with the prehensile tip and convey them to his paws or mouth." The use of the tail for grasping and conveying an object has been observed in the case of the opossum. A captive specimen from southern Illinois was supplied with autumn leaves placed in his box cage for his comfort. One morning Leon L. Pray, who relates the incident (1921, Jour. Mammal., vol. 2, pp. 109-110), observed the opossum "pacing around his beat with a large bunch of leaves tightly rolled up in his long, prehensile tail. He carried this bundle so long, around and around in tireless pace, that I left him without learning the object of his action. Later he repeated this carrying of a bundle of leaves in his tail a number of times. I noticed that he had made a half hearted attempt to build a nest in one corner, but had abandoned the idea and slept anywhere that he happened to be when

drowsiness overcame him." This interesting observation has its parallel in the behavior of a South American opossum, *Monodelphis*, which G. H. H. Tate witnessed in British Guiana (1931, Jour. Mammal., vol. 12, p. 248). The opossum was seen "running between the double canewalls of a hut, dragging with its tail a piece of newspaper. The paper was grasped apparently by curving the entire tail downward over it and was probably being taken to the animal's nest." These observations on the kinkajou and on opossums indicate that mammals may use their tail in unpredictable ways, but there still may be legitimate doubt whether the alleged degree of ingenuity represented by the monkey and the coyote in the accounts associated with these two animals is ever attained.

Having seen a bumblebees' nest ravaged over night by the skunk, which has been caught repeatedly by others in acts of this kind, I suspect that this animal may be an enemy also of stingless bees, but I find no record of such devastations in Cabrera and Yepes (1940). The same work omits mention, too, of honey as a food of the South American bear *Tremarctos ornatus*, and one can only tentatively surmise, therefore, that this bear may be an enemy of stingless bees, although evidence is still, it would seem, lacking.

Lizards are coupled with birds by Saint-Hilaire (1830, p. 373) as enemies of our bees. According to Brunet (cited by Raveret-Wattel, 1875, pp. 749, 753; Girard, 1879, p. 712) small arboreal reptiles known in Brazil as "lagartiscos" lie in wait at the entrance of hives and seize in passage the outgoing and returning worker bees. To protect the bees from these reptilian enemies hives are suspended from the roofs of dwellings (Raveret-Wattel, 1875, p. 749). One of these creatures (*Hemidactylus mabouina*) was observed by Peckolt (1893, p. 581) close to a *Melipona* nest and, when the reptile was killed later on, remains of *Melipona* bees were noted among the stomach contents.

Although the instance that follows concerns not the hives of stingless bees but rather those of the genus *Apis*, it seems in order to cite in this section, as an example of a strange association, the presence in beehives of African green tree snakes. Members of the Wadshagga tribe of the Kilimandjaro region are

ardent bee-keepers, and Gutmann (1909, p. 207), who lived among them, stated that, when a hive is opened, there is frequently found occupying it a reptile of that character, which, the author claimed, is a consumer of honey, a conclusion that seems very problematical. Anyone whose hive is infested by a tree snake looks upon the presence of the snake as an omen of impending death. Accordingly he will not partake of the honey but makes a point of selling it to someone living at a distance with whom he has no ties of friendship.

Fish, given the opportunity (which can be only of casual occurrence), eagerly devour

stingless bees luckless enough to fall into the water. Rau stated (1933, p. 28) that dozens of fish jumped out of the water of Gatun Lake, Canal Zone, to snap up the disturbed inmates of a *Trigona* nest on one of the tiny islets (some of them no bigger than a *jardiniere*) that dot the surface of the lake near Barro Colorado Island. The victims were members of the subgenus *Pariamona*.

However reposeful nature may seem to harassed mortals seeking escape from the combats of life, it has its intranquil aspects, and the existence of a stingless bee, in view of many enemies, is rarely placid and uneventful.

FORAGING AND MATERIALS FORAGED

NECTAR AND POLLEN

Many pages back we left the stingless bees engaged in their flight of orientation, ready to set forth for the distant fields. Yet it seemed desirable before following them on their quest to give an account parenthetically of the different castes that make up the citizenship of the hive and also to treat of the enemies of the hive. Some of these enemies, as we have seen, are actually residents of the hive itself and as such constitute a part of the life of the community. Even those enemies that live apart from the bees usually give evidence of their hostile action only in the proximity of the hive. Accordingly it seemed logical to treat of these matters first but, now that they are disposed of, we are glad to turn from an account of the defense of the realm and destructive combat to the pursuits of peace and provident tasks.

Foremost among the things that stingless bees seek on their excursions are nectar and pollen, the essential food supply of the colony. Flowers, next to the actual nest of these bees, prove the best collecting ground of the melitologist, for it is also the collecting ground *par excellence* of bees themselves. Differences in the quality of the honey of different species prompted F. Smith (1863a, p. 499) to the conclusion that "each species confines itself to particular flowers, never visiting any other kind." On the other hand, Schrottky (1901, pp. 215-216) believed that with the

exception perhaps of the very tiny *Trigona* (those 2 to 3 mm. long) none of the Meliponidae show partialities for particular plants. The floral records have not as yet been comprehensively noted and, until more details are available, it is difficult to say whether in its floral visits a given species is oligolectic or not, but Smith's conclusion would not seem to be generally applicable. It is possible that some species, such as *Lestrimelitta limão* (F. Smith), are partial in their visits to poisonous plants, for the honey of some stingless bees (more especially that of *limão*) frequently causes illness. According to von Spix and von Martius (1828, p. 542) the honey of the same species may be noxious or good depending on the season of the year and the flower from which the nectar has been gathered. Certain species of stingless bees (particularly those of the subgenus *Oxytrigona*) were reported by H. Müller as frequenting ill-smelling plants by preference (1875b, p. 48) and those with oily secretions (1874, p. 32).

What seems not unlikely is that some stingless bees, at least, show a certain fidelity to a given bloom in their successive visits from flower to flower, but without precluding a like devotion to some other plant during that plant's period of ascendancy. At any rate, F. Poey (1852, p. 159), in examining the provision jars of *Melipona beecheii* variety *fulvipes* Guérin, found pollen that was white, yellow, saffron, and chocolate colored, but the contents of each jar were uniform, not

mixed. Poey drew the conclusion that the difference in coloration from jar to jar was due to a difference of age of the stored pollen, but I think it equally likely that this range of color is ascribable to the fact that the pollen may have come from different plants and, if so, then the bees were faithful at a given time to one species of plant and later to another. This interpretation finds support through the observations of Salt (1929, p. 434), who in a nest of *Melipona interrupta* variety *salti* Schwarz found that: "The pollen ranged in colour from gamboge and yellow ochre to light brown, orange, and dull red. Usually each pot contained pollen of about the same basic colour, though sometimes there were small masses of other colours scattered in it. The odour of the pollen varied from pot to pot, probably differing, like the colour, with the flowers from which it was collected." In a nest of a variety of *Trigona* (*Cephalotrigona*) *capitata* variety *zexmeniae* Cockerell there was a somewhat comparable diversity of coloration in the pollen from pot to pot. "The two lower," stated Salt (1929, p. 441), "contained bright orange, almost vermilion, pollen; the two upper a dark gamboge or light brown pollen, dull in tone, in one pot all the same, in the other speckled with dull light yellow." There were only four pollen pots in all. For what it may be worth I might add that pollen brought into a nest of *Trigona* (*Tetragona*) *nigra* variety *paupera* (Provancher) on Barro Colorado Island, Canal Zone, during two and one-half hours of the morning of March 2, 1933, was according to my field notation "almost invariably of a pale yellow color. One load, however, was pink and two other loads were orange colored." A total of 118 loads of pollen were delivered during this time (9:30 A.M. to 12 noon).

That different species of stingless bees have different floral preferences was the conclusion of Michener in a recently issued paper (1946, p. 181) which is heartily commended to the reader. Michener indicated, however, that "perhaps because of the need by these colonial bees for a continuous food supply in a region [Panama and the Canal Zone] where very few plants bloom continuously throughout the year, the species of meliponine bees are not oligolectic."

As indicative of the selectivity of these

bees, Michener mentioned a colony of *Melipona favosa* variety *phenax* Cockerell which chose as its pasturage the flowers of an unidentified herbaceous plant growing at a distance of 200 feet or more from its nest, and this notwithstanding the fact that a small flowering tree of *Dalbergia brownii* was only about 150 feet away while in closest proximity, within 10 feet of the nest, was a blooming *Solanum* bush. Although both of these plants were neglected by *phenax*, they found favor with another species of stingless bee, namely, *Melipona interrupta* variety *triplaridis* Cockerell.

Among *Trigona* Michener found further evidence of floral selectivity. On four different flowering plants growing within a very few feet of one another there were four different species of this genus, three of these species, at least, with a pronounced preference of its own. *Trigona* (*Nannotrigona*) *testaceicornis* variety *perilampoides* Cresson was visiting in numbers *Simsia grandiflora*. On the flowers of *Mentzelia aspersa*, only "a couple of feet away," *Trigona* (*Trigona*) *fulviventris* Guérin was garnering its harvest. A few *Trigona* (*Tetragona*) *jaty* F. Smith evidenced their partiality by frequenting the flowers of a small weed, also only a few feet distant. Visiting a fourth plant, *Ipomoea triloba*, was an undescribed variety of *Trigona* (*Partamona*) *testacea* closely related to variety *cupira* F. Smith. This last-mentioned bee was, however, less exclusive in its floral tastes than the other three species, for its foragers were likewise active on the *Mentzelia*, and an occasional individual even turned its attention to the *Simsia*.

Additional instances are offered by Michener of distant visits by certain species of *Trigona* to favored food plants but neglect of the less desirable granaries immediately at hand, which nevertheless proved attractive to other species. However, I refrain from drawing further upon Michener's interesting paper (1946, pp. 179-197) in this connection, being hopeful that the reader not already familiar with it may turn to it not only for fuller elucidation of the flower visiting habits of stingless bees but for a perusal of many other observations that throw light on these bees and their ways.

Ordinarily it is the worker that one en-

counters on flowers, but of five specimens of *Trigona (Partamona) testacea* variety *nigrior* Cockerell collected by R. G. Donald on flowers of *Antigonon leptopus* at St. Augustine, Trinidad, British West Indies, on January 16, 1945, one was a male. Mr. Donald wrote me in reply to an inquiry regarding this male: "All five were picked by hand from the flowers of *Antigonon leptopus*; dozens of these bees could be seen at any time during the day feeding at the bush in question but I am unwilling to say more than that the male specimen was at rest on, if not actually feeding at, one of the flowers."

In their foraging, bees not only find essential food, they make possible the perpetuation of the floral world as we know it, acting as agents of pollination. But in general this service is taken for granted. It is usually only when some plant of economic importance is maintained through the visits of bees that more than passing mention is made of the service. It is of interest to note that, whereas artificial pollination has been resorted to in the case of the extensively cultivated *Vanilla planifolia*, the vanilla of commerce, it is claimed that in its native home in Mexico and Central America this valued plant is fertilized through the agency of stingless bees (Rolfe, 1895, p. 174; 1896, p. 442). Stingless bees of many varieties, without specification of name, are mentioned by Delteil (1884, p. 9) as pollinators of vanilla not only in Mexico but also in French Guiana. It may well be, however, that stingless bees are not the exclusive agents of pollination of *Vanilla planifolia*, for Girard (1878, p. 6) has a statement to the effect that "the *Vanilla* plants, transported to Haiti, yielded fruits and seeds only after the introduction of bees [evidently an allusion to the honeybee] into the island." But even if Girard's statement is accepted and the honeybee supplements the efforts of the stingless bees in pollinating this plant, vast stretches of geologic time must have passed before this aid on the part of the Old World honeybee was available in the New World tropics.

Certainly stingless bees visit plants of many different groups. Ducke recorded the finding of them on *Amaranthaceae*, *Compositae*, *Solanaceae*, *Labiatae*, *Verbenaceae*, *Melastomaceae*, *Sapindaceae*, *Mimosaceae*,

Papilionaceae, *Piperaceae*, *Orchidaceae*, *Cyperaceae*, *Cucurbitaceae*, *Connaraceae*, *Rubiaceae*, *Acanthaceae*, *Myrtaceae*, *Passifloraceae*, *Bombacaceae*, *Hernandiaceae*, *Euphorbiaceae*, *Meliaceae*, *Burseraceae*, *Araceae*, *Graminaceae*, *Capparidaceae*, *Musaceae*, *Palmaceae*, *Rosaceae*, *Bixaceae*, *Malvaceae*, and *Tiliaceae* (Ducke 1901, pp. 30-32, 49-51; 1902a, pp. 322-326; 1906b, pp. 52-55). Marianno (1911, pp. 75, 84, 106, 128, 135) added other plant groups to the total favored by stingless bees: *Anacardiaceae*, *Aurantiaceae*, *Papaveraceae*, *Terebinthaceae*, *Urticaceae*, *Dilloniaceae*, *Caprifoliaceae*, and *Guttiferae*. Some of the botanical names here recorded have been superseded and are now in the synonymy. Nevertheless, it has seemed best to leave them as they originally appeared.

These records would seem to indicate that stingless bees taken as a whole have not been unenterprising in their floral explorations whatever may be the partialities of the individual species. In connection with the discussions of the several species and varieties in later sections of this monograph, mention is made of the floral visits of each species in so far as such visits are known.

Of *Trigona (Trigona) ruficrus* (Latreille), at least, it has been recorded that, not content with visiting the nectaries in the usual manner, this bee robs plants of their liquid sweets by perforating the area of the plant where these treasures are located (Marianno, 1910b, p. 20; 1911, p. 129; H. von Ihering, 1903, p. 264). In this respect *ruficrus* resembles certain bumblebees, especially *Bombus affinis* and *Bombus terrestris*, which similarly take short cuts in tapping the nectar supply. Although *Trigona (Trigona) fulviventrifera* variety *fulviventrifera* Guérin does not actually "jimmy" its way into the floral treasure room after the manner of the burglar *ruficrus*, it is not reluctant to share the nectar that such acts of house-breaking make available. Dr. J. C. Bequaert wrote me that in Guatemala he observed *fulviventrifera* stealing the nectar of the cultivated coffee plant through perforations in the tube of the corolla that had been made by some other despoiler.

On the other hand, it is easy to exaggerate the depredations and forget the good acts. Bondar, writing of the enemies of the cocoa tree (1940, p. 129), stated that he had heard

suggestions to the effect that *Melipona* is injurious to the flowers but never had he found evidence to support this accusation and personally he was of the conviction that, as an agent of pollination, it was to be classed as beneficent.

In gathering nectar and pollen the stingless bees show a rare persistence. Even under inclement conditions some species will venture forth. For a fuller mention of these evidences of devotion to a task and the reserves of floral food that as a result are stored up, the reader is referred to the section on distant voyages, especially pages 161-162.

HONEY

There are no ethical restraints when one colony of stingless bees or individual members of such a colony find opportunity to pilage the provision stores of a colony that lends itself to exploitation (Rau, 1933, pp. 26-27), and honey, even if of alien manufacture, is usually acceptable. Honey of *Apis* was the food that H. Müller (1875b, p. 52) fed his colony of *Trigona* (*Tetragona*) *jaty* variety *jaty* F. Smith both in transit from Brazil and after its establishment in Germany. Brunet noted that, whenever honey or wax was available, different Meliponidae arrived in numbers to partake of these stores even though their nests were distant 200 meters. Once, when he placed a honeycomb on a table, this comb was completely ravaged by *tataira* variety *flaveola*, member of the subgenus *Oxytrigona*. Notwithstanding the removal of the comb the bees still persisted in coming in great numbers even on the following day, whirling about the space where they had found the comb previously. Drory, too, recorded the avidity with which *flaveola* pillaged the honey supply that he set out for it. Thousands of these bees, he stated, were at once responsive to the lure, but the true producers of the honey kept discreetly at a distance while their obnoxious rivals made away with the store (Drory, 1874, p. 284).

A curious exception to this general partiality for honey is the indifference to it manifested by *Trigona* (*Tetragona*) *nigra* variety *paupera* (Provancher). On Barro Colorado Island, Canal Zone, Lutz (1933, p. 2) offered honey as well as many other things usually

attractive to stingless bees to a colony of this meliponid without luring any of its members.

WATER AND PERSPIRATION

Stingless bees visit puddles to lap up water (Strand, 1909, p. 235) and, as do bees of the family Halictidae, they also suck perspiration. In reading the field notes of the members of the Oxford University Sarawak (Borneo) expedition one cannot fail to be impressed with the number of the collected specimens of *Trigona* that were taken "near sweat and water" (Schwarz, 1937, pp. 281-328, pls. 2-7). Some of the smaller stingless bees, such as *Trigona* (*Hypotrigona*) *duckei* Friese and *Trigona* (*Plebeia*) *minima* Grubbs, have been designated "sweat bees" because of their persistent visitations to lap this fluid. The habit is by no means confined, however, to the small members.

In addition to lapping sweat, it is stated by Brown and Lidstone (1878, p. 76) that "some tiny ones [possibly members of the subgenus *Hypotrigona*] would cause a constant annoyance during the hottest part of the day by persisting in drinking the moisture of our eyes." Indeed in Brazil the bees that have this habit are designated "lambe olhos" or "eye lickers" (Ducke, 1925, p. 342; Guenther, 1931, p. 297). In Malaya Pagden observed *Trigona* (*Tetragona*) *thoracica* F. Smith flying around a hot sulphur spring (Schwarz, 1939c, p. 105).

SECRECTIONS OF INSECTS

The sweet secretions of certain insects are also relished. In the case of at least two members of the subgenus *Oxytrigona*, namely, typical *tataira* F. Smith and *tataira* variety *mediorufa* Cockerell, it has been noted that the bees exploit membracid nymphs for their exudations (H. Müller, 1873, p. 201), and it seems probable that the habit may be general throughout this subgenus, the forms of which are so closely related to one another.

As Müller's account of this habit is the first record of the kind to be noted in connection with stingless bees and is also one of the most informing, it deserves to be quoted:

"He [F. Müller] found the pedunculi of the flowers of *Cassia multijuga* pretty frequently occupied by societies of larvae of

this species [later, 1874, p. 31, identified by Rogenhofer as a member of the genus *Potnia* Stål, probably *indicator*] closely crowded together. Among these larvae there was present a great number of the above-mentioned *Trigona*, marching all the day long amongst and upon them. When taken between the fingers the larvae of *Membracis* immediately emitted a little drop of a limpid fluid from the upward bent tip of their abdomen—probably a sweet fluid, for the sucking of which the larvae are visited by the *Trigona*."

Oxytrigona is, however, not the only subgenus among the stingless bees that exemplifies this habit. Indeed no subgenus has offered more instances of this predilection than the subgenus *Trigona*. At least four different members of this group have been detected in association with insects that secrete delectable fluids. The type species of the genus, *Trigona (Trigona) amalia* (Olivier), has been observed on three occasions in the company of membracids (Cockerell, 1920c, p. 465; Salt, 1929, p. 449; 1945, an unpublished observation by H. Fleming in Venezuela). Furthermore Dr. W. Weyrauch has written me that he saw *Trigona (Trigona) hyalinata* variety *amazonensis* (Ducke) licking the fluids of Homoptera, and Ducke long previously (1906a, p. 18) reported that the same source of liquid apparently is tapped by what he interpreted as *Trigona argentata*.¹ Ducke went on to say that observations in substantiation of the fact that *argentata* uses small Homoptera as milk cows were being initiated in the garden of the Museu Goeldi in Pará, Brazil, and would in course of time be published by the museum. The fourth species of the subgenus *Trigona* that has been found exploiting nymphs of Homoptera is *ruficrus* (Latreille). This instance is also due to the vigilance of Ducke (1925, p. 346).

The subgenera *Oxytrigona* and *Trigona* are evidently homopterophilous as these multiple instances tend to establish, but at least yet a third subgenus is known to share this partiality for insect products. According to Silvestri (1902b, p. 152), *Trigona (Parta-*

mona) testacea variety *cupira* F. Smith laps the saccharine excretions of the homopteron *Aethalion reticulatum* Linnaeus.

The following account is given by Lutz (1924b, p. 507) of a similar habit indulged in by yet another stingless bee, regrettably not now traceable as to subgenus: "While waiting for a car in the Canal Zone I noticed many *Trigona* flying in and out of a brush pile in which grew a rambling *Solanum*, a plant related to our potato and tomato. Thinking there might be a nest there, I carefully parted the brush and found not a nest but the thing that was attracting the bees. It was a colony of immature 'insect Brownies,' small, curiously shaped creatures belonging to the family Membracidae, that were feeding on the *Solanum* and having their secretions fed on in turn by the bees."

At Nyctheroy (Niteroi), Brazil, Bristowe (1925, p. 488) observed *Melipona* bees tickling an *Aethalion* to obtain its exudation. Bristowe's "*Melipona*" includes *Trigona*.

An animated picture of the voracity of stingless bees in consuming the exudations of other insects is given by Guenther (1931, p. 301), unfortunately without designation of species: "In the garden at Olinda I saw some 'Sugar Cicadas' in all stages of development, from the youngest wingless forms, on the twigs of a bush, sucking the sweet sap. The bees were profiting by their presence; whole troupes of them were running over the Cicadas, licking their bodies, which exuded a sweet liquid, and eating their saccharine droppings."

Hermann Müller, Ducke, and Lutz called attention to the fact that this behavior is reminiscent of that of certain ants which attend colonies of plant lice in much the same way. The habit, however, is also shared by other social bees, for *Apis mellifera* Linnaeus as well as *Bombus terrestris* (Linnaeus) and *Bombus terrecola* Kirby are all fond of the sugary excretions of aphids. Indeed, it is claimed that honeydew is the chief cause of dysentery in the honeybee.

Insect secretions, it would seem, may in some cases largely displace nectar as a source of honey, for, according to D. T. Fullaway and N. L. H. Krauss (1945, "Common insects of Hawaii," p. 169) the honeydew of the sugar cane leaf-hopper, before this insect was

¹ By *argentata* Ducke probably meant *Trigona (Trigona) fulviventris* variety *guyanensis* Cockerell or, less likely, *Trigona (Trigona) hypogaea* Silvestri. The reader is referred to pages 232 and 332.

brought to the verge of extinction through parasites and predators, furnished about two-thirds of the forage of the honeybee in areas of the Hawaiian Islands. One can but wonder whether a diversion from floral to insect exploitation on such a scale ever occurs in the case of the stingless bees.

Closely allied to the visits of stingless bees to membracids is a record put forth diffidently by Fiebrig (1908, p. 377) who "seemed even to remember" that he had come upon meliponids using wax that had been removed from coccids. Here may be indeed an interesting extension of the tendency of stingless bees to exploit other insects, but the putative observation needs substantiation.

ANIMAL JUICES

The carcasses of animals are frequented, primarily, it would seem, for their juices. It was the impression of H. Müller (1874, p. 32; 1875b, p. 48) that *tataira* of the subgenus *Oxytrigona* is especially attracted to meat and putrifying dead animals. But while *Oxytrigona* is partial to these unsavory sources of liquid, many other stingless bees have shown a like perverted taste. Among the persistent visitors of the carcasses of animals is the member of the subgenus *Trigona* that Dücke (1902b, p. 313; 1906a, p. 18) designated *argentata* (see footnote, p. 232). This bee he likewise repeatedly observed gorging itself on dead caterpillars. Because of this partiality on the part of Dücke's "*argentata*" for animal products, von Buttel-Reepen (1903b, p. 99; cited by Dücke, 1906a, p. 18) raised the question whether this bee might be considered a flesh eater, but Dücke answered this question in the negative, indicating that it is the animal fluids, not the flesh, to which the insect is partial. On the other hand, Lutz observed *Trigona* (*Trigona*) *hypogea* variety *hypogea* Silvestri, *Trigona* (*Trigona*) *pallida* variety *pallida* (Latreille), and *Melipona* *interrupta* variety *oblitescens* Cockerell visiting the skinned carcass of a snake and added: "Apparently they not only sucked the fluids but also carried off small bits of the flesh" (in Cockerell, 1920c, p. 460). It is possible, nevertheless, that the transported particles were to serve not as food but as building materials—part of that odd assortment of

objects that are blended into the conglomerate edifice that stingless bees construct.

Although stingless bees give evidence of a partiality for insect and animal juices, they are not the only bees that are sometimes lured from their floral visits to return to the diet of their sphecoid relatives among the wasps. The occasional interest shown by the honeybee and by certain bumblebees in insect secretions has been mentioned, but during a recent visit to Chichen-Itza, State of Yucatan, Mexico, I was startled to note a specimen of the beautiful *Euglossa cordata* (Linnaeus) exploring with interest the juicy remains of two crushed flies.

SUGAR, FRUITS, AND RESINS

A pleasanter source of edible supplies than putrid meat juices is sugar cane, which is listed by H. Müller (1875b, p. 48) as attractive to *tataira*, but sugar is also favored by other species—*amalihea*, for instance (Burmeister, 1853, p. 219), as well as certain *Partamona*. *Trigona* (*Trigona*) *ruficrus* (Latreille) prefers "the yellow Moscovade sugar" to white sugar, according to Peckolt (1894, p. 224), but it gathers both kinds eagerly. Brown sugar that had been accidentally soaked proved a constant attraction to presumably meliponid bees during a trip made by Brown and Lidstone on the Rio Tapajós, Pará, Brazil (1878, p. 165). Jam was a lodestone to *Trigona* (*Trigona*) *pallida* (Latreille) possibly because of its sugar content (Cockerell, 1920c, p. 463).

On the other hand, sugar consumption sometimes produced ill consequences. Von Humboldt (1811, p. 242) noted that when the bees (presumably he is speaking of the stingless bees) took the juice of sugar cane to excess, they became sodden as though intoxicated.

Fruits are sought by stingless bees. On Barro Colorado Island, Canal Zone, a partly peeled banana would soon be dotted over with eager black bees of the subgenus *Partamona* (Schwarz, 1932b, p. 553), and a soft banana proved attractive to *Trigona* (*Trigona*) *corvina* Cockerell (Rau, 1933, p. 36). *Trigona* (*Trigona*) *amalihea* (Olivier) scars the young fruit of the banana (Salt, 1929, p. 440).

In spite of the records of the partiality of stingless bees for sweet things, the insects do not always react in the expected manner. Much to his surprise Lutz found (1933, p. 2), when starting experiments with stingless bees on Barro Colorado Island, Canal Zone, that he could lure them neither with sweetened water, even when it was placed in close proximity to the nest, nor with white sugar, nor brown sugar, nor a host of tidbits such as maple syrup, sweetened orange syrup, grenadine, and ripe fruits. Even meat and lard were tried but without result. The bee upon which in particular these attentions were lavished so ineffectually was *Trigona* (*Tetragona*) *nigra* variety *paupera* (Provancher).

Citrus orchards are often subject to attack, particularly by certain members of *Trigona* subgenus *Trigona*. In the rogues' gallery of marauders such *Trigona* as *amalthaea* (Olivier), *trinidadiansis* (Provancher), *trinidadiansis* variety *silvestriana* Vachal, *ruficrus* (Latreille)—all members of the subgenus *Trigona*—receive invidious distinction for the ravages they inflict (Marianno, 1910b, p. 20; 1911, pp. 126, 129; H. von Ihering, 1912, p. 3; Salt, 1929, p. 440; M. Bates, 1933, p. 47; Rau, 1933, p. 37; Myers, 1935b, p. 134).

Although the fruit may be attacked, the principal injury is to the trunk and main branches of the tree, which the bees scar and strip of their bark. They have the habit, too, of nipping off the young green shoots. These destructive activities are prompted by the fact that the mutilations make accessible the gummy secretions of the tree, which are eagerly sought by the bees as building material for their nests.

Attacks of this nature are not confined to orchards. The bark not only of orange trees but of *Hibiscus*, *Cajanus*, and *Quassia* is attacked by certain species of stingless bees in Brazil, especially by one designated "arapuá" (probably *Trigona ruficrus*) according to Raveret-Wattel (1875, p. 754). The bark of the *Eucalyptus* tree is sometimes similarly scarred, *Trigona* (*Trigona*) *trinidadiansis* (Provancher) having been caught incriminatingly in this act on more than one occasion. The uses to which such *Eucalyptus* products may sometimes be applied was indicated by Hockings (1884, p.

155), who stated that the "karbi" (interpreted as *Trigona carbonaria* F. Smith) and the "kootchar," described by Cockerell as *Trigona cassiae*, two of the stingless bees of Australia, build the batumen plates with which they partition off their nest "of *Eucalyptus* gum mixed with rubbish, which is added to from time to time, and gradually becomes very thick and hard."

Illustrative of the destruction wrought by *Trigona* (*Trigona*) *trinidadiansis* variety *trinidadiansis* (Provancher) on the bark of trees is an observation communicated to me by R. G. Donald, who during his residence in Trinidad, British West Indies, had a chance to note the foraging of this species. It attacked not only the ornamental tree *Poinciana regia*, from which it obtained a resin-like secretion, but also a non-ornamental tree the name of which could not be ascertained. In the trunk and main branches of this tree there were about 20 holes that the bees visited, and Donald found that the hole extended inward for a depth slightly greater than the diameter of the hole. "The margins of these cavities were scarred with recent wounds inflicted by the bees in order to stimulate the flow of the viscid secretion, which they carried away on the hind tibiae as they might carry pollen." It was the conclusion of Donald that the original incisions must have been made during the early growth of the tree, and that they had been kept open by continuous foraging of the bees over the years. This conclusion was strengthened by the fact that there were no evidences of recent attacks upon the younger branches or twigs. The bees defended this foraging ground as aggressively as though it had been their nest. Attacks on the bark of the pigeon pea (*Cajanus indicus*) by *trinidadiansis* are also mentioned by Donald.

Very quickly do the stingless bees become aware of the treasured supplies made available to them. In Cuba, if a manaju tree (*Garcinia cornea*) has its bark injured, with resulting exudation of resin, *Melipona beecheii* variety *fulvipes* Guérin will be on the scene, even if the spot be a well-concealed one, before the day is over. F. Poey (1852, p. 159), who supplied this observation, made mention also of the resin of *Calophyllum*

calaba as among the favored supplies sought by *fulvipes*, and he inferred that further probable quarries of resinous material were *Cameraria latifolia*, *Achras sapota*, *Achras tinctoria*, and *Bumelia nitida*.

Meliponid bees were noted by Fiebrig (1908, pp. 376-377) in Paraguay gathering the sticky sap of *Sapium biglandulosum*, which welled forth from wounds in the bark, probably inflicted by the bees themselves. It is interesting to learn from Fiebrig's further comments that the native population of the region employs this sap as bird lime. *Ficus indica*, suspected by F. Poey (1852, p. 163) of being one of the plants whose sap is sought by the bees, is likewise of service to man as a source of bird lime. Various species of *Ficus* as well as species of *Artocarpus* and of *Clusia* were mentioned by Brunet as likely sources of resin (Raveret-Wattel, 1875, p. 744). Among plants attractive to stingless bees because of their resinous exudations F. Müller (1875, p. 296) listed *Pterocarpus* and "biciuba."

Although the viscid sap exuding from the wounded trunks or branches of trees is the principal source for resinous material, the surface of leaves is scraped in the search for waxy products. The leaves of a plant designated "gandú" are mentioned by F. Poey (1852, p. 161) as being attractive to *Melipona beecheii* variety *fulvipes* Guérin because of a waxy secretion. H. Müller (1875b, p. 52) observed *Trigona* (*Tetragona*) *jaty* variety *jaty* F. Smith in the act of removing a thin layer of wax from the upper surface of the leaves of a rose bush.

TAR, GREASE, OIL, AND VARNISH

In addition to gums and resins other sticky substances are not neglected by the assiduous searchers of building materials. Tar and grease (Rau, 1933, pp. 26, 37) serve different species. *Trigona* (*Trigona*) *pallida* variety *pallida* (Latreille), one of the species that Rau observed loading grease, was also noted gathering oil (Wheeler, 1913, p. 3; Schwarz, 1932b, pp. 552-553), and usually with such eagerness that the bees more or less transformed themselves from fulvous insects into motley specimens of black and fulvous by bespattering themselves with the adherent fluid. Varnish was eagerly gathered

by *Melipona fasciata* variety *scutellaris* Latreille and other stingless bees, according to Drory (1874, p. 284; 1877, p. 145), who also mentioned that in nests of stingless bees (both *Melipona* and *Trigona*) stores of propolis are frequently piled up in a corner of the hive in preparation for later use. H. Müller, too (1875b, p. 43), recorded storage of heaped-up resin, and Schulz (1905a, p. 203) found a chamber filled with propolis in a nest of *Melipona marginata* variety *marginata* Lepeletier.

EXCREMENT AND URINE

Many stingless bees have the unpleasant habit of visiting excrement, which they use as building materials for their nests. For this purpose dung of carnivorous and of herbivorous animals, of birds, and even human excrement, are used. In southern Brazil, Marianno found *Trigona* (*Trigona*) *ruficrus* (Latreille) engaged in removing the undigested plant particles from manure of bovines, probably for employment in the construction of the involucre of the nest (1911, p. 127). In this connection it may be noted that macerated leaves were found by Weyrauch in the structure of the involucre of nests of *Trigona* (*Trigona*) *trinidensis* variety *trinidensis* (Provancher) in Peru.

Urine, also, is a lure to stingless bees (Spegazzini, 1909, p. 65; Strand, 1912a, p. 11) although the honeybee, too, has been observed visiting pigsties for these unsavory fluids. Spegazzini was at first inclined to believe that this repulsive habit was based on the insect's desire to obtain salt, but he rejected this explanation because he had never noted a stingless bee visiting salt that had been strewn over the earth by muleteers for the benefit of their animals. One can share Spegazzini's distaste for the honey of stingless bees on reading in his account that these insects also exploit the sores of the pack animals in their indiscriminating search for liquid. Dirty moist garments are also visited according to the same observer, although it is probably the moisture rather than the dirt that is the attraction.

COFFEE

From the human standpoint a more understandable predilection of stingless bees is for

coffee. At any rate Bell (1899, p. 232) recorded that they are very fond of it and that "it is very difficult to drink a calabash of it without swallowing them by the dozens." One wonders whether the sugar content of the beverage may have been the attraction or whether the coffee in itself proved irresistible.

UNUSUAL THINGS

Among unusual things carried off by stingless bees Rau mentioned (1933, pp. 26, 27) "moist bread" and "a substance which appeared to be red lead that plumbers use for leak-proofing joints." Bits of Christmas cake were taken into their nest by members of a colony of *Trigona (Partamona) testacea* variety *helleri* Friese (H. von Ihering, 1903, p. 275). Truly the variety of things seized upon by stingless bees either for the building of the nest or the replenishment of their larder is quite amazing, but "old stinking cheese" mentioned by H. Müller (1874, p. 32; 1875b, p. 48) as being attractive to that perverted epicure, *Trigona (Oxytrigona) tataira* variety *tataira* F. Smith, is among the strangest things listed.

Yet an observation made by G. H. H. Tate in Papua as to the unpredictable responses of stingless bees transcends all others in its bizarre character. Tate, a member of the Archbold expedition of 1936-1937, stated to me that at a camp newly made June 7, 1936, a little below the junction of the Black River with the Palmer River, numerous stingless bees entered an uncorked killing bottle containing cyanide, presumably attracted by the fumes, and met their death there, although no obstacle was placed to their egress and they might readily have escaped. The bees were all of one species: *Trigona (Tetragona) planifrons* F. Smith. The bees crowded around the bottle and the number that entered it and succumbed to the fumes filled the bottle compactly to the depth of about 1 inch.

THINGS TOSSED OUT OF THE NEST

Not only are things carried into the nest but things are also carried out. Slain insects whose hardihood in penetrating into the hive has been rewarded with death are removed and, in case they are too large to be

transported, are fragmented before eviction (Raveret-Wattel, 1872d, pp. 684-685; Drory, 1873d, p. 70). Inquilines are sometimes treated with equal ruthlessness, and forcible mass ejections of unwanted tenants of the nest occur and are noted elsewhere in this paper (p. 93). Removal of dead individuals of the colony (H. von Ihering, 1903, p. 203; Rayment, 1932a, p. 252; 1935, p. 538) and the banishment of the drones (p. 55) may also be mentioned. In Java, Jacobson repeatedly observed workers of *Trigona (Tetragona) iridipennis* F. Smith engaged in removing what he inferred were pupae from cells that had been inadvertently damaged and dropping these pupae outside the nest (cited by Friese, 1914a, p. 46). Jacobson likewise noted in the case of another colony of *iridipennis* that the workers removed, in addition to dead individuals of the community, small pellets of a yellowish green substance that he interpreted as excrement (cited by Friese, 1914a, pp. 54, 55). Unlike the honeybee, which refrains from voiding her excreta in the hive, the stingless bees desecrate their home (Drory, 1874, p. 284; Marshall, 1898, p. 147). Drory indicated that after the excrement dries, it is partitioned and borne out of the nest. According to Rayment (1932a, p. 248) there is "always a busy traffic carrying out round flat cakes of brown excrement, which is held by the mandibles, and tucked well in under the head." Ejection of debris from the nest was noted by the same author as continuing until well past seven o'clock of an October evening. From a nest of *Melipona fasciata* variety *rufiventris* Lepeletier the bees removed old particles of wax (H. von Ihering, 1903, p. 203). I have myself noticed workers of *Trigona (Tetragona) nigra* variety *paupera* (Provancher) on several occasions carrying particles clasped in their mandibles out of the nest. A newly installed colony of *Trigona (Tetragona) iridipennis* F. Smith in a small crevice in a wall was observed carrying out small pieces of mortar and depositing them at some distance from the hive (George, 1934, p. 5).

HOW MATERIALS ARE TRANSPORTED

Earthen materials are extensively used in the nests of stingless bees, especially those of the genus *Melipona*, and hence moist clay

or mud is among the things transported to the nest on those convenient burden bearers, the hind tibiae.

More than 80 years ago H. W. Bates (1863, pp. 43-45) gave a graphic description of the way in which workers of what he interpreted as *Melipona interrupta* variety *fasciculata* F. Smith loaded themselves with the essential materials for nest construction: "The rapidity and precision of their movements while thus engaged are wonderful. They first scrape the clay with their mandibles; the small portions gathered are then cleared by the anterior paws and passed to the second pair of feet, which in their turn convey them to the large foliated expansions of the hind shanks, which are adapted normally in bees, as everyone knows, for the collecting of pollen. The middle feet pat the growing pellets of mortar on the hind legs to keep them in a compact shape as the particles are successively added. The little hodsmen soon have as much as they can carry and they then fly off."

The sequence of transfer from mandible to fore legs, thence to the inner side of the middle legs, and finally to the outer side of the tibiae of the hind legs is that followed also in the gathering of resinous material as observed by Williams (1928a, p. 172), and that author stated that "when the material is not very adhesive, as muddy sand, it is the fore and not the third pair of legs that braces the bee, the middle pair gathering up the sand

and placing it on the corbicula of the third." Von Buttel-Reepen, too, observed stingless bees using their middle legs to pack loads on the corbiculae of the hind legs, "just as we see this leg action in the honeybee" (1915, p. 144).

While the hind tibiae are usually employed for more or less solid materials, meliponid bees may also carry burdens clasped between the head and fore legs. It was thus that *Trigona* (*Tetragona*) *jaty* variety *jaty* F. Smith bore into the nest the little pellets of wax that it fashioned from larger balls of wax placed by H. Müller (1875b, p. 52) to each side of the nest entrance. L. E. Cheesman (1933, p. 58) mentioned that the *Trigona* she had under observation would bring up gum, "a drop at a time from the depths of the nest," for the purpose of rebuilding the destroyed portal, and she added that the "glistening yellow bubble" was carried in the jaws. In cleansing the nest of any unwanted materials Tomaschek (1879, p. 584) noticed that the bees bore out the particles clutched in their mandibles, and Rayment (1932a, pp. 246-247) made a comparable observation in connection with the cleansing of nests of *Trigona carbonaria* F. Smith which were suffering from a heavy infestation of the larvae and pupae of a small fly. Possibly this method of conveyance in which the mandibles rather than the hind legs play a part is employed mainly in transferring objects that are in the nest or in close proximity to it.

PLATE 5

1. Nest of *Trigona* (*Trigona*) *trinidensis* variety *trinidensis* (Provancher) at San Ramon, Peru, built in a stone wall. Externally it resembled "a large deposit of cow dung glued to the wall." The exposed part projected beyond the wall for a distance of 14 cm. Before this picture was taken the front of the nest was removed to expose the interior. Arrow points to brood cells. Photograph by W. Weyrauch.

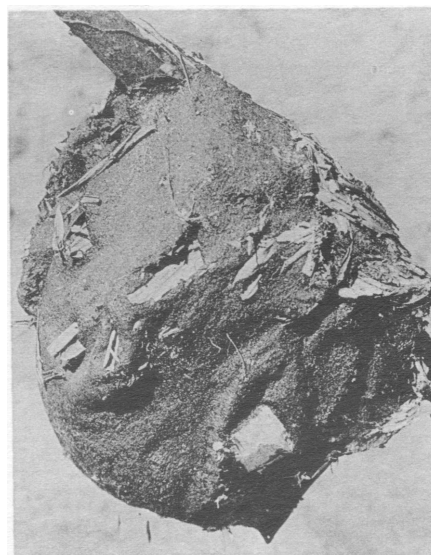
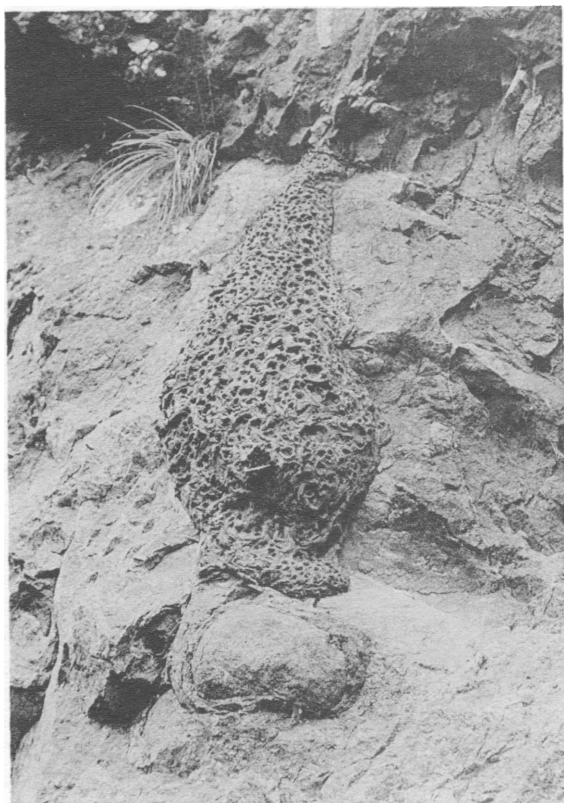
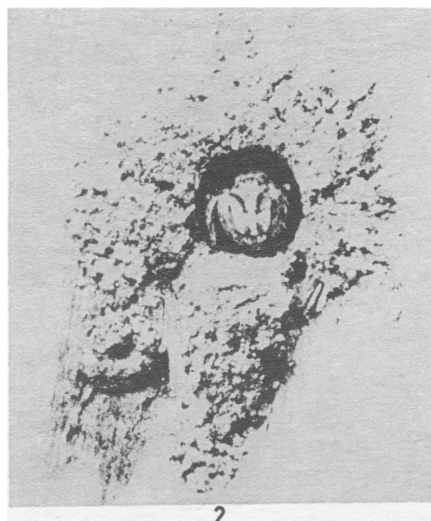
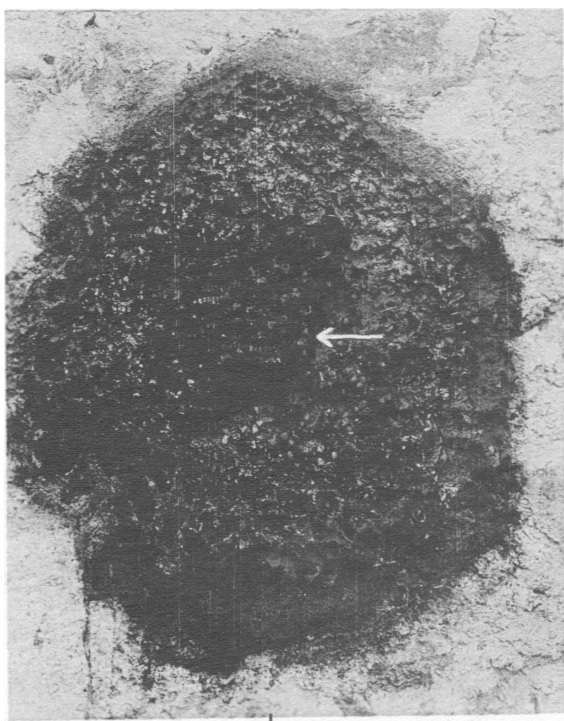
2. Bee guarding the portal in a nest of *Melipona marginata* Lepeletier. After José Marianno.

3. Entrance to a nest of *Trigona* (*Trigona*) *recura* F. Smith at the foot of an old tree at San Ramon, Peru. A tunnel-like front structure of black granular resin held fast to the ground the dead leaves that were lying about. The tunnel entered into a hollow root, which was used by the

bees as a passageway to the nest. Photograph by W. Weyrauch.

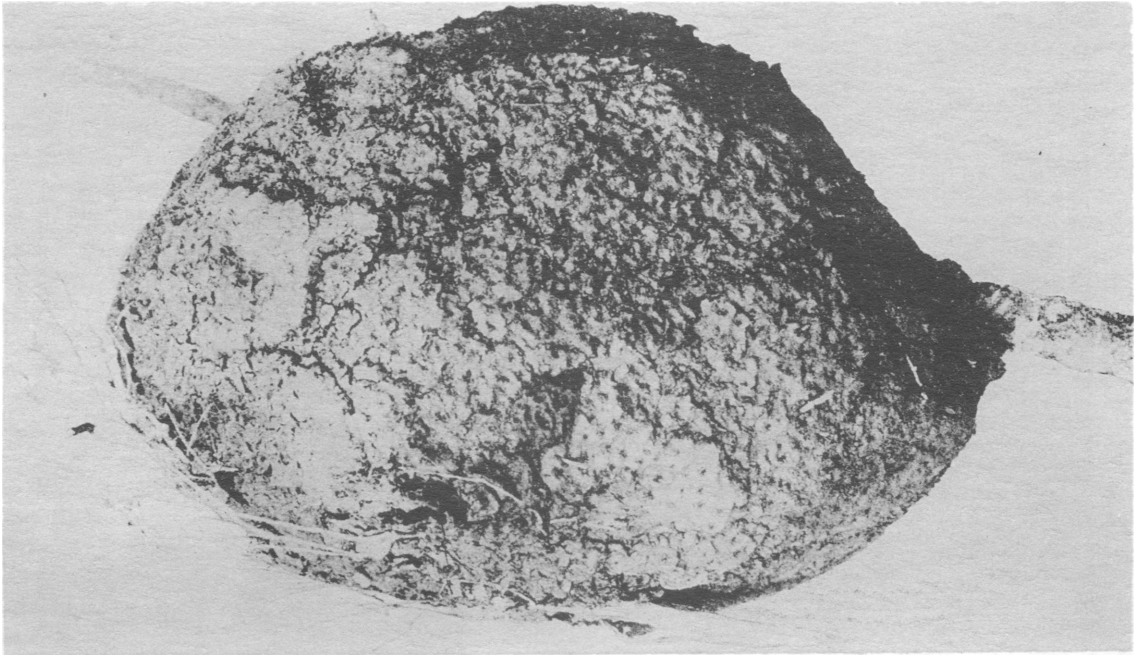
4. Nest of *Trigona* (*Trigona*) *hyalinata* variety *amazonensis* (Ducke), at San Luis de Shuaro, Valle de Chanchamayo, Peru, located on a rock wall 6 meters in height. The nest itself was about 1 meter in length and rose brown in color. Photograph by W. Weyrauch.

5. Nest of *Trigona* (*Paratrigona*) *opaca* variety *pacifica* Schwarz on the dead limb of a tree. Weyrauch, in an accompanying field note, stated that the colony was originally started in a birds' nest but that the material constituting the birds' nest was carried off progressively as the wax structure of the bees tended to expand. Birds' nests are favored nesting sites of *pacifica*. Photograph by W. Weyrauch.

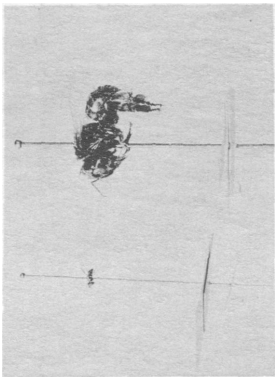


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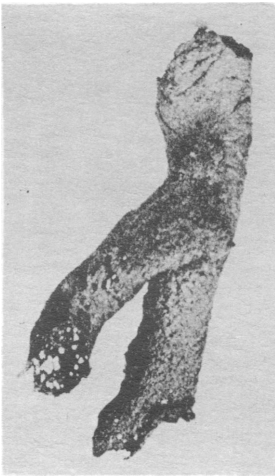
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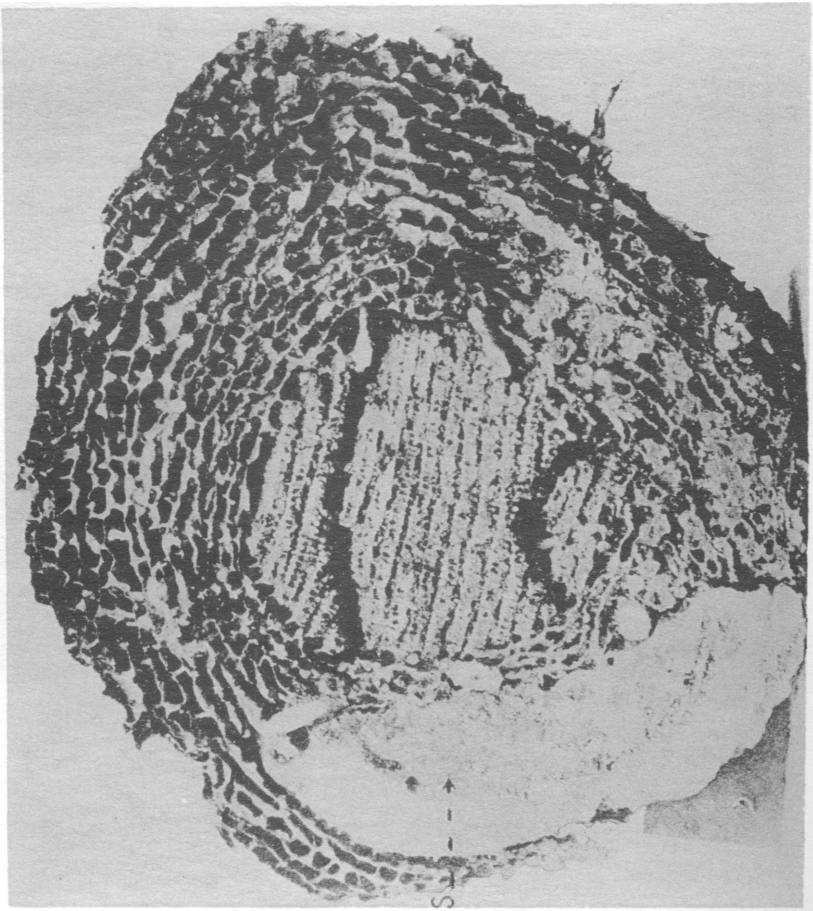
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2



1



4

But on longer trips, too, the mandibles sometimes serve for transport. It is the mandibles that F. Poey (1852, p. 160) mentioned as an occasional carrying agent in the case of *Melipona beecheii* variety *fulvipes* Guérin. This bee would paste the softer adhesive resin to its hind tibiae, but, when it was a question of solid particles of resin, these were seized with the jaws. It was observed by von Buttel-Reepen (1915, p. 144) that both wax and propolis were borne home between the mandibles by Meliponidae. Earthen materials, too, are sometimes transported after this manner. Occasional stingless bees were observed by F. Müller (1875, p. 296) bearing earth on their hind tibiae, but for good measure they were carrying homeward also a mouthful of this substance.

These authentic observations stand in contrast with those of Pedro Cieza de León, whose "La crónica del Perú" first appeared in 1553. This early chronicler described the stingless bees as entering the flight tube with "their little wings laden with what they have collected from the flowers" (1864, pp. 90-91), a concept more poetic than accurate. The hind legs of the stingless bee, not the wings, are the agency through which are carried in the main not only the materials required in nest construction but also the pollen harvest that the bees have laboriously gathered. Often the hind tibiae are made conspicuous by the massed pollen grains with which these joints are bulging, sure proof of a successful quest.

A COMPARATIVE STUDY OF THE HAMULI IN THE SOCIAL BEES, WITH SPECIAL REFERENCE TO THE MELIPONIDAE

We have discussed the foraging of stingless bees in the last section. It seems not inappropriate to discuss in the present section the equipment of the bees for flight and the differences, if any, in the flight equipment of the different castes. Especially will the discussion be directed to the little wing hooks or hamuli that are located on the anterior margin of the hind wing of Hymenoptera (the order in which the bees are included) and that fit into a fold along the posterior margin

of the fore wing, thus uniting the two wings in flight and strengthening the wing beat. The number of these hamuli differ considerably between different Hymenoptera, and even within a single group, such as the stingless bees, there are differences in the number from species to species. Question may be raised as to the significance, if any, of these disparities.

Tarlton Rayment, in his interesting volume entitled "A cluster of bees" (1935, p.

PLATE 6

1. Bifurcated flight tube of *Trigona iheringi* Friese, which has been interpreted as a synonym of *Trigona (Scaptotrigona) postica* Latreille. Such eccentricities of nest architecture are uncommon. After H. von Ihering.

2. Extremes of size among species of stingless bees. A worker of *Melipona flavipennis* F. Smith, one of the larger members of the genus *Melipona*, compared with a worker of *Trigona (Hypotrigona) duckei* Friese, which, it is claimed, is the smallest of all known bees. Both bees are equidistant from the camera, although, owing to the different thickness of the pins, the illusion is unfortunately created that the smaller insect is the more distant. *Trigona (Hypotrigona) duckei* is so tiny that it was originally described from a specimen that lodged in the eye of an entomologist and the describer ex-

pressed doubt whether any net was fine enough to hold it. Photographed in the American Museum.

3. Most stingless bees build concealed nests in tree hollows and other suitable cavities. In contrast, *Trigona (Trigona) ruficrus* Latreille persistently erects its nests in the open, attached to the branches of trees, which frequently penetrate the structure. After H. von Ihering.

4. Interior of a nest of *Trigona (Trigona) ruficrus* Latreille, showing the centrally placed combs surrounded by the labyrinthine involucre. To the left (S) is the scutellum, a mass of earthen material mixed with wax and resin that is a not unusual feature in nests of this species. Frequently the scutellum occupies an even larger part of the nest than is indicated in the photograph. After H. von Ihering.

512), reaffirms a statement made some years earlier (1932a, pp. 183-184): "After a close examination of the wings of bees in hundreds of genera, and many field experiments on their homing capabilities, I regard the number of wing-hooklets as an infallible guide to the 'air range' of the bee. Where the hooklets are four or so, the area of flight is but a few hundred yards; *Microglossella*, for example, has only three weak ones, whereas the hive-bee, with its twenty-two hooklets, will easily return from a distance of seven miles. My experiments showed that many hundreds of worker-bees returned home, in less than twenty minutes, after being liberated from a point in a dense forest, three miles distant. . .

"The Australian species of *Trigona* have only from five to six hamuli, or hooklets, and the neurulation of the wings is largely obsolete; therefore, they are utterly incapable of crossing any moderately extensive natural barrier."

Rayment's conclusions prompted me to reexamine many species of New World and also of Old World *Trigona* with reference to their hamuli, and likewise to take stock of the hamuli in species of the closely related genus *Melipona*. The New World species of *Trigona* normally have at least five hamuli in each lower wing, as do the Old World species, although in very exceptional cases an individual may have as few as four. Even the smallest of all the species [and what has been asserted to be the smallest of all the bees, *Trigona* (*Hypotrigona*) *duckei* Friese] has normally five hamuli. *Trigona* species considerably larger than *duckei* often have no more than five hamuli, but in general the tendency seems to be for the hamuli to increase in number as the insects grade into larger species, although this generalization cannot be applied in several instances. There is variability within a single species with respect to the number of hamuli, and there is even asymmetry within a single individual, the left lower wing sometimes having more hamuli than the right or vice versa. In a general way it may be said, however, that species small in size tend to have few hamuli; species of more robust build are apt to have more hamuli.

The number of hamuli in the Meliponidae is more closely correlated, in my estimation,

with the body weight of the insect than with the wing length. This may be visualized in a broad way if comparison is made between the equipment of hamuli in species of *Melipona* on the one hand and that in species of *Trigona* on the other. *Melipona* are larger insects than *Trigona*, but their wings are relatively shorter. In fact, one of the best distinctions drawn between the two genera is that workers and males of *Trigona* tend to have wings extending well beyond the tip of the abdomen, while workers and males of *Melipona* have wings that ordinarily do not extend to the tip of the abdomen. What the *Trigona* lack in body size is thus compensated for to some extent by their relatively greater wing length. In some species—for instance, *Trigona* (*Trigona*) *trinidensis* variety *trinidensis* (Provancher) and *Trigona* (*Trigona*) *williana* Friese—the wing length is not merely relatively greater but also actually greater than that of at least some of the species of *Melipona*, while several species of *Trigona* in addition to *trinidensis* and *williana* challenge in wing length *Melipona marginata* Lepeletier, the smallest member of *Melipona*. But even *trinidensis* and *williana* have notably fewer hamuli than has the shorter-winged *Melipona marginata*. Of the species of *Melipona* only *marginata* and its varieties seem to average in the worker caste as low as between nine and 10 hamuli, and in only one of the forms of *marginata*, namely, *illustris*, have I come upon individual specimens with as few as eight hamuli. A number as low as eight must be looked upon as excessively rare in *Melipona*, and even nine hamuli are a rarity in all species of *Melipona* other than *marginata*. For most species of *Melipona* (see table 1) the low limit in hamuli per wing in the worker caste is 10 or 11, more rarely, 12 or 13. Among insects of large size, such as those comprising the *Melipona interrupta* group, an occasional specimen was found having as many as 16 hamuli, but such individuals seem to be as rare as those in the *Melipona marginata* group that have as few as eight hamuli, and the extreme range within *Melipona* would seem, therefore, to be from eight to 16, although it is possible that an occasional "freak" exceeds these limits. In general, species of small size tend in *Melipona* to have

TABLE 1
SPECIES OF *Melipona*

Species	Caste	Range in Number of Hamuli per Wing	Average Number of Hamuli per Wing	Number of Wings Counted	Range in Body Length (in mm.)
<i>beecheii</i> var. <i>beecheii</i>	Worker	9-12	10.43	60	8.50-11.00
	Queen	10-11	10.25	2	8.00 (virgin)
<i>beecheii</i> var. <i>fulvipes</i>	Male	10-11	10.34	3	9.00-10.00
	Worker	9-12	10.44	25	8.00-10.00
<i>beecheii</i> var. <i>obscuripes</i>	Male	10-12	10.75	4	8.50- 9.50
<i>fasciata</i> var. <i>abunensis</i>	Worker	11-12	11.10	7	9.00-11.00
<i>fasciata</i> var. <i>belizeae</i>	Worker	12-13	12.33	3	10.00-10.50
<i>fasciata</i> var. <i>boliviana</i>	Worker	10-12	11.17	6	9.00- 9.50
<i>fasciata</i> var. <i>cramptoni</i>	Worker	12	12.00	2	10.00-11.00
<i>fasciata</i> var. <i>eburnea</i>	Worker	12-13	12.55	11	9.75-11.50
<i>fasciata</i> var. <i>fasciata</i>	Worker	11-13	12.16	16	9.50-10.00
<i>fasciata</i> var. <i>fusca</i>	Worker	11-13	11.30	10	9.00-10.00
<i>fasciata</i> var. <i>fuscipes</i>	Worker	12-14	13.25	4	10.00-12.50
<i>fasciata</i> var. <i>lateralis</i>	Worker	11-12	11.50	2	9.00-10.00
<i>fasciata</i> var. <i>melanopleura</i>	Worker	11-14	12.40	45	9.00-11.50
<i>fasciata</i> var. <i>melanoventer</i>	Worker	11-13	11.88	4	9.00-10.00
	Male	10-11	10.50	1	9.75
<i>fasciata</i> var. <i>merrillae</i>	Worker	11-13	12.17	9	10.00-10.50
<i>fasciata</i> var. <i>mimetica</i>	Worker	11-13	11.75	4	10.00-11.00
<i>fasciata</i> var. <i>nigrescens</i>	Worker	11-13	12.00	9	8.00- 9.50
	Queen	10-11	10.50	2	7.00- 8.00 (virgin)
<i>fasciata</i> var. <i>paraensis</i>	Worker	12-13	12.13	4	10.00-10.50
<i>fasciata</i> var. <i>pseudocentris</i>	Worker	10-13	11.35	28	7.50-10.00
	Male	11	11.00	1	8.25
<i>fasciata</i> var. <i>rufescens</i>	Worker	12-13	12.40	6	9.00-11.50
<i>fasciata</i> var. <i>rufiventris</i>	Worker	13-14	13.25	2	10.50-11.00
<i>fasciata</i> var. <i>scutellaris</i>	Worker	10-13	11.29	23	8.00-10.00
<i>fasciata</i> var. <i>seminigra</i>	Worker	12-13	12.50	3	9.50-11.50
<i>fasciata</i> var. <i>trinitatis</i>	Worker	11-13	12.13	4	9.50-11.00
<i>favosa</i> var. <i>baeri</i>	Worker	11-13	12.13	4	9.25-11.00
	Worker	10-12	11.00	8	7.50- 8.75
<i>favosa</i> var. <i>favosa</i>	Male	11	11.00	4	7.25- 8.50
<i>favosa</i> var. <i>lunulata</i>	Worker	10-13	11.10	20	7.25-10.00
<i>favosa</i> var. <i>orbigny</i>	Worker	9-11	10.13	4	7.50- 8.50
	Worker	10-12	11.00	5	7.25- 9.00
<i>favosa</i> var. <i>peruviana</i>	Male	10-11	10.60	5	7.50- 8.50
	Worker	9-12	10.80	5	7.50- 8.00
<i>favosa</i> var. <i>phenax</i>	Worker	10-13	11.60	41	7.50- 9.00
<i>favosa</i> var. <i>variegatipes</i>	Male	9-12	10.75	14	7.50- 8.50
	Worker	10-12	11.00	3	6.50- 7.50
<i>flavipennis</i>	Worker	12-15	13.42	18	10.00-12.50
	Queen	12-14	13.00	3	11.00-11.50 (virgin)
<i>interrupta</i> var. <i>fasciculata</i>	Male	13-15	14.00	3	11.00-12.00
	Worker	13-15	13.65	12	10.50-13.50
<i>interrupta</i> var. <i>grandis</i>	Worker	12-16	13.62	20	11.00-13.50
<i>interrupta</i> var. <i>interrupta</i>	Worker	13-15	13.60	5	10.50-13.50

TABLE 1—(continued)

Species	Caste	Range in Number of Hamuli per Wing	Average Number of Hamuli per Wing	Number of Wings Counted	Range in Body Length (in mm.)
<i>interrupta</i> var. <i>mañaosensis</i>	Worker	13-14	13.42	6	10.50-13.00
	Male	13	13.00	1	12.00
<i>interrupta</i> var. <i>oblitescens</i>	Worker	12-15	13.59	35	10.00-12.00
<i>interrupta</i> var. <i>salti</i>	Worker	12-14	12.50	5	10.50-12.00
	Queen	9-11	10.38	4	10.00-10.50 (virgin)
	Male	11-13	12.40	5	11.00-12.00
<i>interrupta</i> var. <i>tripilaridis</i>	Worker	11-16	13.32	34	10.00-12.50
<i>mandacaia</i>	Worker	10-11	10.50	1	8.00
<i>marginata</i> var. <i>amazonica</i>	Worker	10-11	10.10	5	7.00- 8.00
<i>marginata</i> var. <i>illustris</i>	Worker	8-10	9.00	4	6.75- 7.25
<i>marginata</i> var. <i>marginata</i>	Worker	9-10	9.46	12	6.00- 7.25
	Queen	8	8.00	2	8.50 (gravid)
	Male	9-11	9.75	4	6.50- 7.25
<i>marginata</i> var. <i>torrida</i>	Worker	9-10	9.25	2	6.25- 7.00
<i>marginata</i> var. <i>tumupasa</i>	Worker	10	10.00	1	7.00
<i>puncticollis</i> var. <i>ogilviei</i>	Worker	10-13	11.25	2	8.00- 8.75
<i>puncticollis</i> var. <i>puncticollis</i>	Worker	11	11.00	1	8.00
<i>quadrifasciata</i> var. <i>anthidioides</i>	Worker	11-13	11.86	14	7.50- 9.50
	Queen	11	11.00	2	8.25- 8.50
	Male	12-13	12.50	1	9.25
<i>quadrifasciata</i> var. <i>quadrifasciata</i>	Worker	10-13	11.68	34	7.50- 9.50
	Queen	10	10.00	1	10.00 (gravid)
	Male	10-12	10.75	2	9.00
<i>quinquefasciata</i>	Worker	11-13	11.85	10	8.50-10.00
	Male	11-13	12.00	3	9.25-10.00
<i>schencki</i> var. <i>picadensis</i>	Worker	10-14	12.00	20	8.25- 9.50
	Queen	10-11	10.50	2	11.50 (gravid)
	Male	12-13	12.33	3	7.75- 9.50
<i>schencki</i> var. <i>schencki</i>	Worker	11-14	11.89	9	7.75- 9.50
	Queen	10-11	10.50	1	10.00 (gravid)
	Male	11-13	11.75	2	8.50- 9.75

fewer hamuli than species of large size (see table 1). In many cases only a very few specimens of *Melipona* were available in given subspecies. To offset to some extent this inadequacy, a practice was adopted of counting the number of hamuli on each wing. As asymmetry from wing to wing is not uncommon, a count of each wing has somewhat the effect of doubling the available specimens. The same practice was followed in the case of *Trigona* (tables 2 and 3), as well as in the other tables offered. In table 2 only the subgenera considered taxonomically in the present treatise have been included. How-

ever, the remaining subgenera of *Trigona* present no exceptions to the limited equipment of hamuli indicated in table 2, although now and then an individual of *Scaptotrigona* has as many as nine hamuli.

Among the New World *Trigona* I have found occasional individuals in the species *quadripunctata* and *capitata* crossing into the 10 zone of hamuli, which constitutes the low limit for most *Melipona*. The Old World species *bocandei* and *thoracica* are others that now and then have as many as 10 hamuli. Cockerell erected a subgenus *Meliponula* for *bocandei* and expressed the opinion that the

TABLE 2
SPECIES OF NEW WORLD *Lestrimelitta* AND *Trigona*

Species	Caste	Range in Number of Hamuli per Wing	Average Number of Hamuli per Wing	Number of Wings Counted	Range in Body Length (in mm.)
<i>Lestrimelitta</i>					
<i>ehrharti</i>	Worker	5	5.00	2	5.75
	Male	5	5.00	2	6.50
<i>limão</i>	Worker	4-7	5.22	148	5.50- 6.25
	Queen	4-5	4.60	7	7.00-10.50 (gravid)
	Male	5-6	5.35	14	5.50- 6.00
<i>Trigona</i> (subgenus <i>Trigona</i>)					
<i>amalthaea</i>	Worker	4-7	5.19	200	4.75- 5.50
	Queen	5	5.00	2	9.50 (gravid)
	Male	5	5.00	10	4.75- 5.50
<i>amapana</i>	Male	4-5	4.88	8	5.00- 5.50
<i>chanchamayoënsis</i>	Worker	5-6	5.10	128	4.50- 6.00
	Male	5-6	5.17	6	5.25
<i>compressa</i>	Worker	4-5	4.99	93	5.50- 6.75
	Male	5-7	5.25	280	5.50- 6.25
<i>corvina</i>	Worker	4-7	5.07	250	4.75- 5.50
	Queen	5	5.00	4	8.00
	Male	4-6	5.05	181	4.75- 5.50
<i>dallatorreana</i>	Worker	4-6	5.00	76	7.00- 9.00
	Male	5	5.00	2	7.00
<i>dimidiata</i> var. <i>dimidiata</i>	Worker	5-7	6.11	72	7.50-10.00
<i>dimidiata</i> var. <i>venezuelana</i>	Worker	5-7	6.12	25	6.00- 7.50
<i>fulviventris</i> var. <i>fulviventris</i>	Worker	5-6	5.08	250	5.00- 6.50
	Male	5-6	5.15	20	6.00- 6.50
<i>fulviventris</i> var. <i>guianae</i>	Worker	5-7	5.14	154	5.00- 6.50
	Male	4-6	4.94	32	5.50- 6.50
<i>hyalinata</i> var. <i>amazonensis</i>	Worker	5-6	5.66	136	6.25- 7.50
<i>hyalinata</i> var. <i>branneri</i>	Worker	5-6	5.07	118	5.00- 6.50
	Male	5-6	5.50	2	5.00
<i>hyalinata</i> var. <i>hyalinata</i>	Worker	4-7	5.42	125	5.00- 6.50
<i>hypogea</i> var. <i>hypogea</i>	Worker	5-7	5.12	244	4.00- 6.25
<i>nigerrima</i>	Worker	5-7	6.00	124	6.00- 7.00
	Queen	6-7	6.50	2	7.50 (virgin)
	Male	5-6	5.89	9	6.50- 7.00
<i>pallida</i> var. <i>ferricauda</i>	Worker	5-6	5.14	14	4.50- 6.00
<i>pallida</i> var. <i>muzoënsis</i>	Worker	5	5.00	12	5.00- 6.00
<i>pallida</i> var. <i>pallida</i>	Worker	5-7	5.20	160	4.50- 6.00
	Queen	5	5.00	2	8.50 (gravid)
	Male	4-5	4.92	12	5.00- 5.50
<i>recurva</i>	Worker	4-6	5.08	173	4.25- 5.75
	Male	4-6	5.00	185	5.00- 7.00
<i>ruficrus</i>	Worker	4-6	5.08	140	5.50- 6.50
	Male	5	5.00	2	5.50
<i>trinidadensis</i> var. <i>silvestriana</i>	Worker	5-7	6.15	81	6.50- 8.50

TABLE 2—(continued)

Species	Caste	Range in Number of Hamuli per Wing	Average Number of Hamuli per Wing	Number of Wings Counted	Range in Body Length (in mm.)
<i>trinidadensis</i> var. <i>trinidadensis</i>	Worker	5-8	6.18	330	7.50-11.00
	Queen	6	6.00	1	10.00 (gravid)
<i>williana</i>	Male	5-6	5.75	4	8.05-11.00
	Worker	4-7	5.15	140	6.50- 9.00
	Male	5	5.00	8	8.00
<i>Trigona</i> (subgenus <i>Paratrigona</i>)					
<i>haeckeli</i>	Worker	5	5.00	6	3.50- 4.00
<i>impunctata</i>	Worker	4-5	4.98	57	4.25- 5.00
	Male	5	5.00	6	4.50
<i>isopterothila</i>	Worker	5	5.00	16	4.50
	Male	5	5.00	2	4.50
<i>lineata</i> var. <i>lineata</i>	Worker	5-6	5.06	154	3.50- 4.50
	Male	4-5	4.88	8	3.75- 4.50
<i>lineata</i> var. <i>nuda</i>	Worker	5-7	5.08	142	3.50- 4.50
<i>opaca</i> var. <i>anduzei</i>	Worker	4-5	4.98	180	3.75- 4.50
<i>opaca</i> var. <i>guatemalensis</i>	Worker	4-6	4.97	70	3.75- 4.25
<i>opaca</i> var. <i>lineatifrons</i>	Worker	5	5.00	2	4.50
<i>opaca</i> var. <i>opaca</i>	Worker	5-6	5.03	40	3.75- 4.50
	Male	5	5.00	2	4.50
<i>opaca</i> var. <i>ornaticeps</i>	Worker	5	5.00	2	3.50
<i>opaca</i> var. <i>pacifica</i>	Worker	5-6	5.09	124	3.50- 4.50
<i>petropolis</i>	Worker	5	5.00	123	3.50- 4.50
	Male	5-6	5.10	10	5.00- 5.50
<i>prosopiformis</i>	Worker	5-6	5.13	30	4.50- 6.00
	Male	5	5.00	2	6.00
<i>Trigona</i> (subgenus <i>Schwarziana</i>)					
<i>quadripunctata</i> var. <i>bipartita</i>	Worker	7-10	8.46	56	5.00- 6.50
	Male	7-9	8.00	16	5.50- 7.50
<i>quadripunctata</i> var. <i>quadripunctata</i>	Worker	8-10	8.64	50	5.50- 6.50
	Queen	8	8.00	2	11.00 (gravid)
	Male	7-9	8.42	12	5.50- 7.50
<i>Trigona</i> (subgenus <i>Parapartamona</i>)					
<i>zonata</i> var. <i>brevipilosa</i>	Worker	5	5.00	6	5.00- 6.00
<i>zonata</i> var. <i>caliensis</i>	Worker	5	5.00	4	5.50
<i>zonata</i> var. <i>tungurahua</i>	Worker	5	5.00	2	6.50
<i>Trigona</i> (subgenus <i>Cephalotrigona</i>)					
<i>capitata</i> var. <i>capitata</i>	Worker	7-9	7.96	150	6.75- 8.00
	Queen	7-8	7.75	4	8.50 (virgin)
	Male	7-10	7.84	19	7.50- 9.00
<i>capitata</i> var. <i>eburneiventer</i>	Worker	7-8	7.81	16	6.75- 8.00
<i>capitata</i> var. <i>femorata</i>	Worker	7-9	8.02	44	7.00- 9.00
<i>capitata</i> var. <i>zexmeniae</i>	Worker	7-9	8.06	36	7.00- 9.00
	Queen	7-8	7.67	3	9.00 (virgin) 11.00 (gravid)
	Male	7-10	8.00	36	7.00- 9.00
<i>Trigona</i> (subgenus <i>Oxytrigona</i>)					
<i>tataira</i> var. <i>flaveola</i>	Worker	6-8	6.61	107	4.25- 6.25
<i>tataira</i> var. <i>mediorufa</i>	Worker	5-7	6.06	106	4.50- 5.50
<i>tataira</i> var. <i>mellicolor</i>	Worker	5-8	6.09	182	4.00- 6.50

TABLE 2—(continued)

Species	Caste	Range in Number of Hamuli per Wing	Average Number of Hamuli per Wing	Number of Wings Counted	Range in Body Length (in mm.)
<i>tataira</i> var. <i>mellicolor</i>	Male	4-6	5.39	58	4.50- 6.75
<i>tataira</i> var. <i>mulfordi</i>	Worker	6-8	6.50	24	4.50- 5.50
<i>tataira</i> var. <i>obscura</i>	Worker	5-7	6.16	105	4.00- 5.25
<i>tataira</i> var. <i>tataira</i>	Worker	5-8	6.43	75	4.75- 6.50
	Male	6-7	6.50	30	4.75- 5.75
<i>Trigona</i> (subgenus <i>Scaura</i>)					
<i>latitarsis</i>	Worker	4-7	5.10	200	3.25- 4.25
	Queen	5-6	5.50	2	6.50
	Male	5-6	5.07	15	3.75- 4.50
<i>longula</i> var. <i>longula</i>	Worker	5	5.00	14	5.50- 6.00
<i>Trigona</i> (subgenus <i>Mourella</i>)					
<i>caerulea</i>	Worker	6-8	7.14	14	4.75- 5.75

TABLE 3
OLD WORLD SPECIES OF *Trigona*

Species	Caste	Range in Number of Hamuli per Wing	Average Number of Hamuli per Wing	Number of Wings Counted	Range in Body Length (in mm.)
<i>alinderi</i> var. <i>alinderi</i>	Worker	8	8.00	6	6.05-7.75
<i>alinderi</i> var. <i>mimica</i>	Worker	8	8.00	4	7.00-7.75
<i>apicalis</i> var. <i>apicalis</i>	Worker	6-9	7.07	130	5.25-7.75
	Male	7-8	7.50	2	7.00
<i>apicalis</i> var. <i>binghami</i>	Worker	6-8	7.06	46	5.00-6.50
<i>apicalis</i> var. <i>melanoleuca</i>	Worker	7-8	7.23	44	5.25-7.00
<i>apicalis</i> var. <i>peninsularis</i>	Worker	6-8	7.00	40	5.25-6.50
<i>atomella</i>	Worker	5	5.00	4	2.50
<i>atricornis</i>	Worker	6-8	7.25	12	4.00-5.00
<i>atripes</i> var. <i>atripes</i>	Worker	5-7	6.00	120	4.00-5.00
	Male	6-7	6.50	4	6.00
<i>atripes</i> var. <i>collina</i>	Worker	6-7	6.27	100	4.50-4.50
	Male	6	6.00	2	5.50
<i>atripes</i> var. <i>fuscibasis</i>	Worker	5-8	6.78	46	4.50-6.00
<i>australis</i>	Worker	6-7	6.25	4	3.75-4.00
<i>beccarii</i>	Worker	7-8	7.67	28	5.00-6.50
	Male	8	8.00	2	6.75
<i>bocandei</i>	Worker	8-11	9.11	18	6.00-8.50
<i>bottegoi</i>	Worker	5	5.00	12	2.00-2.50
<i>cambodiensis</i>	Worker	6-7	6.40	20	4.75-5.50
<i>cameroonensis</i>	Worker	7-8	7.67	10	6.50-7.50
<i>canifrons</i>	Worker	6-8	7.02	216	5.00-8.25
<i>carbonaria</i>	Worker	4-6	5.18	40	3.00-4.00
	Male	4-5	4.83	6	3.00-4.00
<i>cassiae</i>	Worker	6	6.00	3	4.00
<i>cincta</i>	Worker	5-6	5.11	18	3.25-4.00
<i>clypeata</i> var. <i>zebra</i>	Worker	6-7	6.17	12	4.25-5.00
	Queen	7	7.00	2	8.00
					(gravid)
	Male	6	6.00	2	5.00

TABLE 3—(continued)

Species	Caste	Range in Number of Hamuli per Wing	Average Number of Hamuli per Wing	Number of Wings Counted	Range in Body Length (in mm.)
<i>conradti</i>	Worker	6-7	6.13	8	5.50-6.00
<i>denoiti</i> var. <i>denoiti</i>	Worker	5-7	6.08	12	4.50-5.50
	Male	6-7	6.50	2	6.00
<i>denoiti</i> var. <i>katangensis</i>	Worker	6-7	6.56	16	4.50-5.50
<i>erythra</i>	Worker	6	6.00	2	6.00
<i>erythra togoënsis</i>	Worker	6-7	6.13	24	5.00-5.75
<i>erythrogastra</i>	Worker	6-8	7.30	62	6.00-7.50
<i>fimbriata</i> var. <i>aliceae</i>	Worker	7-8	7.50	2	7.50
<i>fimbriata</i> var. <i>fimbriata</i>	Worker	7-9	7.38	100	6.75-8.75
<i>fimbriata</i> var. <i>versicolor</i>	Worker	6-7	6.50	2	6.75
<i>flavibasis</i>	Worker	6	6.00	2	4.00
<i>flaviventris</i>	Worker	7-8	7.50	2	6.50
<i>fusco-balteata</i>	Worker	4-6	4.95	130	2.25-3.25
	Male	5	5.00	20	2.50-3.00
<i>geissleri</i>	Worker	5-7	5.38	100	3.75-5.50
	Male	5-6	5.20	10	4.00-5.50
<i>genalis</i>	Worker	7-8	7.38	8	4.50-5.00
<i>gribodoi</i> var. <i>gribodoi</i>	Worker	5-6	5.08	120	2.25-3.25
<i>gribodoi</i> var. <i>braunsi</i>	Worker	5	5.00	4	2.00-2.50
	Male	5	5.00	2	2.50
<i>haematoptera</i> var. <i>dulitae</i>	Worker	7-8	7.25	4	5.75-7.00
<i>haematoptera</i> var. <i>haematoptera</i>	Worker	7-8	7.40	12	6.25-7.00
<i>iridipennis</i> var. <i>iridipennis</i>	Worker	4-6	5.03	130	2.50-4.50
	Queen	4-5	4.50	4	5.00-5.25 (gravid)
	Male	4-5	4.93	14	3.75-4.25
<i>iridipennis</i> var. <i>valdezi</i>	Worker	5-6	5.11	100	3.50-5.00
	Male	5	5.00	2	4.25
<i>itama</i>	Worker	6-9	7.17	240	5.00-7.00
<i>keyensis</i>	Worker	7-9	8.08	12	6.00-7.25
	Male	7	7.00	2	6.00
<i>madecassa</i>	Worker	4-5	4.86	10	2.00-2.75
	Male	5	5.00	1	2.50
<i>melanocephala</i>	Worker	5-6	5.20	10	3.50-4.75
<i>melina</i>	Worker	5-6	5.20	30	3.75-5.00
<i>moorei</i>	Worker	6	6.00	3	3.50
<i>nebulata</i> var. <i>infusata</i>	Worker	6	6.00	2	6.00
<i>nebulata</i> var. <i>nebulata</i>	Worker	6	6.00	10	4.00-6.00
	Male	6	6.00	2	6.00
<i>nitidiventris</i> var. <i>latipes</i>	Worker	7-8	7.50	4	5.50-6.00
<i>nitidiventris</i> var. <i>nitidiventris</i>	Worker	6-8	7.13	24	5.50-6.50
<i>nitidiventris</i> var. <i>trochanterica</i>	Worker	8-9	8.25	4	5.50
<i>pendleburyi</i> var. <i>klossi</i>	Worker	5-6	5.08	12	2.50-2.75
<i>pendleburyi</i> var. <i>pendleburyi</i>	Worker	5-6	5.38	22	2.50-2.75
<i>planifrons</i>	Worker	6-8	7.25	16	5.25-6.00
<i>sarawakensis</i> var. <i>drescheri</i>	Worker	5	5.00	2	3.50
<i>sarawakensis</i> var. <i>sarawakensis</i>	Worker	5-6	5.21	14	3.50-4.75
<i>scintillans</i>	Worker	5	5.00	4	2.25-2.50
<i>staudingeri</i>	Worker	6	6.00	16	4.50-6.00
<i>terminata</i> var. <i>latebaleata</i>	Worker	6-7	6.25	84	4.00-5.50
<i>terminata</i> var. <i>terminata</i>	Worker	5-9	6.46	42	4.50-5.50
<i>thoracica</i> var. <i>thoracica</i>	Worker	7-11	8.87	126	6.00-9.00
<i>ventralis</i> var. <i>ventralis</i>	Worker	6-7	6.25	12	3.25-3.75

forms of the *bocandei* group are closely related to *Melipona*, "more closely than to the other African species of *Trigona*." The number of the hamuli in *bocandei* (approximately the high limit for *Trigona*) give support to Cockerell's conclusion.

A cursory glance at tables 2 and 3, representing, respectively, some of the New World and Old World *Trigona*, will indicate how relatively few are the number of the hamuli in most of the members of this genus as compared with *Melipona*.

It will be noted that in general the range in the number of hamuli per wing is relatively slight. Where a large number of specimens of a given form are available, a range of as much as four hamuli may be observed between the best equipped and the least equipped individuals. However, the vast majority of specimens show a difference of only one hamulus. Thus, to take an instance, there were examined of *Trigona itama* no fewer than 132 specimens. In some cases the lower wings were mutilated or concealed, so that the actual number of wings studied in these specimens totaled 240 instead of 264. These 240 wings were equipped as follows:

3 wings had 6 hamuli
196 wings had 7 hamuli
38 wings had 8 hamuli
3 wings had 9 hamuli

That the number of individuals of minimum and of maximum equipment is small in cases where the range of hamuli is great may be ascertained by referring to the description of the wing in the case of the several species and varieties included in the Systematic Account.

Unfortunately queens of *Melipona* and of *Trigona* are rare in collections. For the most part, therefore, the conclusions have had to be based on an examination of only one or of, at most, a very few representatives of the royal caste in the limited number of species for which they were available. Not only are the queens poorly represented in collections, but often their wings are frayed, making an accurate estimate of the number of hamuli difficult or impossible. Nevertheless, in every case examined the queens of *Melipona* were found to have a lower average number of hamuli than either their conspecific workers or

males. In most cases the reduction in the number of hooklets was quite emphatic. The queens of *Melipona* tend to be smaller than the other members of the hive, have narrower heads and more reduced wings than the workers, and, in the virgin state at least, have an abdomen no more expansive. The physogastric queens are, of course, more distended and bloated and hence bulkier than the other members of the colony, and it might be argued that, if the hamuli are of aid in more closely uniting the upper and lower wings and thus imparting strength to the united wing beat, nature has treated the queens of this genus with a certain lack of foresight in failing to provide for a time when their pregnant body may require a stronger lifting quality than that adequate in their virgin state. It is to be remembered, however, that it is in all probability the virgin queen in *Melipona* that leads the swarm from the parent hive, not the old queen as in the honeybee *Apis*. Hence the *Melipona* queen is approximately as well equipped for her flight as are her associated workers. Later, when her abdomen is swollen with eggs and her activities are confined to the hive, the need for flight and for flight equipment has passed.

In general the queens of *Trigona*, like the queens of *Melipona*, are less adequately equipped with hamuli than at least the conspecific worker and frequently also the conspecific male. But the differences in equipment of hamuli when they do occur are not so great as they are between queen, on the one hand, and worker and male, on the other hand, in *Melipona*, and in a few instances, as tables 2 and 3 reveal, the queen of *Trigona* is actually better equipped than the other members of the colony. This is what one would have expected on *a priori* grounds, for the queen in the genus *Trigona* is larger (even in the virgin state) than are the worker and the male, and the surprise, therefore, is rather that in so many instances the queen falls behind the worker in number of hamuli.

The honeybee queen likewise is larger in body length and, it might be added, also in wing length than is the worker. Yet it would seem that in the case of this royal mother, too, the equipment of hamuli is inferior to that of her daughters and sons. I have had available

for examination only a limited number of queens of *Apis mellifera* Linnaeus, the total number of wings examined being 51. As the following tabulation reveals the wing of the queens rarely had as many as 21 or 22 hamuli, which is the prevalent equipment of the worker. In the examples before me, at least, no queen had more than 22 hamuli per wing. On the other hand, even the limited number of specimens of the royal caste examined revealed individuals of lower equipment than the specimens of minimum status among the large number of workers studied. The count in the case of the 51 wings of queens showed the following apportionment of hamuli:

1 wing	had 12 hamuli
1 wing	had 13 hamuli
2 wings	had 14 hamuli
9 wings	had 15 hamuli
11 wings	had 16 hamuli
9 wings	had 17 hamuli
8 wings	had 18 hamuli
6 wings	had 19 hamuli
1 wing	had 20 hamuli
2 wings	had 21 hamuli
1 wing	had 22 hamuli

The average for the queen, on the basis of the 51 wings counted, was 16.86 hamuli per wing. In contrast to this figure the average for the worker, based on an examination of 200 wings, was 20.43 hamuli per wing. The 200 wings of workers examined revealed the following:

1 wing	had 15 hamuli
6 wings	had 16 hamuli
10 wings	had 17 hamuli
17 wings	had 18 hamuli
31 wings	had 19 hamuli
35 wings	had 20 hamuli
41 wings	had 21 hamuli
29 wings	had 22 hamuli
13 wings	had 23 hamuli
14 wings	had 24 hamuli
2 wings	had 25 hamuli
1 wing	had 26 hamuli

The drone of the honeybee is seemingly better equipped with hamuli than is the worker or the queen. There was a range of variation in the 35 wings examined from 18 to 26, distributed as follows:

2 wings	had 18 hamuli
8 wings	had 19 hamuli
4 wings	had 20 hamuli
5 wings	had 21 hamuli
7 wings	had 22 hamuli
3 wings	had 23 hamuli
2 wings	had 24 hamuli
2 wings	had 25 hamuli
2 wings	had 26 hamuli

The average based upon the above figures is 21.30 hamuli per wing in the small number of males examined. The figure contrasts particularly sharply with the average recorded for the queen. If the hamuli, as seems plausible, are an aid in flight, the males should have no difficulty in overtaking the queen in that mating flight so fervently described by Maeterlinck.

The honeybee worker, which is rather smaller than the corresponding caste of *Melipona flavipennis* F. Smith, *Melipona interrupta* Latreille, and some of the varieties of *Melipona fasciata* Latreille, is nevertheless distinctly better equipped with hamuli than are they, and even more striking is the disparity between the worker of *Apis* and the worker of *Trigona*. A sharp contrast exists, too, between the honeybee queen as well as the honeybee male when either of these is compared with the corresponding caste in *Melipona* and particularly in *Trigona*. In fact, as compared not only with the Apidae but with the other main group of the social bees, namely, the bumblebees, or Bombidae, the Meliponidae are the least favored by nature in respect to their wing equipment. Table 4 gives a summary of the number of hamuli found in various Nearctic species of *Bombus*, and table 5 a similar survey of certain members of the inquiline genus *Psithyrus* of the bumblebees.

In these tables have been included species of small size and species of large size, and the count has been based on specimens showing as wide a range of stature as possible, yet none of the species of Bombidae listed (and I believe them to be representative) shows an average number of hamuli per wing that is so low as the highest average recorded for any meliponid bee.

It is of special interest, too, in drawing deductions from these tables, to note that, whereas the queen of *Apis* and of *Melipona*,

TABLE 4
NEARCTIC SPECIES OF *Bombus*

Species	Caste	Range in Number of Hamuli per Wing	Average Number of Hamuli per Wing	Number of Wings Counted	Range in Body Length (in mm.)
<i>affinis</i>	Worker	17-27	21.42	50	10.00-16.00
	Queen	25-29	27.34	6	20.00-21.00
	Male	19-23	20.74	23	13.50-16.00
<i>americanorum</i> (= <i>pennsylvanicus</i>)	Worker	19-26	21.80	50	11.00-17.00
	Queen	20-28	24.00	20	19.00-22.00
	Male	18-26	21.08	50	15.00-22.00
<i>bimaculatus</i>	Worker	16-23	19.65	17	10.00-15.00
	Queen	20-26	23.85	20	15.00-20.00
	Male	17-23	19.86	50	10.00-15.00
<i>californicus</i>	Worker	16-22	19.27	15	11.00-14.00
	Queen	20-24	21.67	15	16.00-18.50
	Male	16-23	19.64	11	13.00-16.00
<i>centralis</i>	Worker	14-23	17.96	50	9.00-12.50
	Queen	19-25	21.65	17	12.50-16.50
	Male	15-21	17.78	23	10.00-12.50
<i>edwardsii</i>	Worker	13-21	17.54	50	8.00-12.00
	Queen	18-25	20.83	35	12.00-16.00
	Male	15-20	16.78	50	8.00-12.00
<i>fervidus</i>	Worker	17-22	19.53	60	11.00-15.00
	Queen	19-24	21.35	40	16.50-20.00
	Male	16-24	19.62	50	11.50-18.00
<i>flavifrons</i>	Worker	13-22	16.67	75	7.00-12.00
	Queen	19-23	20.69	13	12.50-15.50
	Male	15-18	16.36	11	9.00-11.50
<i>huntii</i>	Worker	15-22	18.30	50	9.00-13.00
	Queen	19-26	22.49	35	14.00-19.50
	Male	16-21	18.00	37	10.00-13.50
<i>impatiens</i>	Worker	15-24	19.61	75	7.50-15.00
	Queen	21-28	23.92	26	19.00-22.50
	Male	16-23	19.54	50	9.00-14.00
<i>mixtus</i>	Worker	14-20	16.80	50	7.00-11.00
	Queen	20-23	21.33	6	11.50-15.00
	Male	14-20	16.77	26	9.00-14.00
<i>morrisoni</i>	Worker	17-29	22.08	80	12.50-16.50
	Queen	23-27	25.71	7	18.00-22.00
	Male	19-26	22.48	54	13.00-20.00
<i>occidentalis</i>	Worker	16-25	21.05	75	9.00-13.50
	Queen	20-27	24.81	21	14.00-19.50
	Male	16-24	21.24	50	9.50-15.50
<i>rufocinctus</i>	Worker	13-20	16.67	60	8.50-11.50
	Queen	19-25	20.62	24	14.00-16.00
	Male	15-20	17.70	40	10.00-15.00
<i>separatus</i>	Worker	17-24	20.60	10	12.00-16.00
	Queen	23-28	25.15	14	18.00-22.00
	Male	17-25	20.96	25	12.50-17.50
<i>sylvicola</i>	Worker	14-22	17.28	50	8.00-13.00
	Queen	20-25	22.29	17	13.00-16.50
	Male	16-21	17.89	19	9.00-13.50

TABLE 4—Continued

Species	Caste	Range in Number of Hamuli per Wing	Average Number of Hamuli per Wing	Number of Wings Counted	Range in Body Length (in mm.)
<i>ternarius</i>	Worker	13-22	18.48	50	8.50-12.50
	Queen	20-24	21.90	20	15.00-17.50
	Male	14-21	17.87	30	10.00-13.00
<i>terricola</i>	Worker	15-24	20.55	60	9.00-16.00
	Queen	19-27	24.06	17	16.00-21.00
	Male	13-25	21.08	50	10.00-16.50
<i>vagens</i>	Worker	13-22	17.50	60	7.00-14.00
	Queen	19-27	21.85	40	15.50-19.00
	Male	15-21	17.75	60	9.50-14.00
<i>vosnesenskii</i>	Worker	15-20	18.44	9	7.00-14.00
	Queen	21-26	22.80	10	15.50-20.50
	Male	17-21	18.90	10	10.50-14.00

TABLE 5
NEARCTIC SPECIES OF *Psithyrus*

Species	Caste	Range in Number of Hamuli per Wing	Average Number of Hamuli per Wing	Number of Wings Counted	Range in Body Length (in mm.)
<i>ashtoni</i>	Females	19-23	21.26	15	15.50-19.00
	Males	16-22	18.38	21	11.00-15.00
<i>insularis</i>	Females	16-24	20.46	15	12.00-19.00
	Males	15-20	17.00	28	10.00-15.00
<i>laboriosus</i>	Females	20-24	21.80	5	16.00-20.00
	Males	15-20	18.00	9	12.50-15.00
<i>suckleyi (latitarsus)</i>	Females	20-23	21.42	12	15.50-19.00
	Males	14-18	15.77	13	11.50-15.00

and in the majority of instances also the queen of *Trigona*, has fewer hamuli than has the conspecific worker, the bumblebee queens in all cases throughout table 4 are impressively ahead of their associated workers and males in this wing equipment. It may be premature to express an opinion based on so limited a number of specimens examined, but the available data suggest that, in the royal caste of *Melipona*, prevailing also of *Trigona*, and likewise of *Apis* there has been a degeneration not only in such structures as the hind leg and certain other body parts but also in the armature of the hind wing. On the other hand, the bumblebee queen, being differentiated not structurally but mainly as

to size from her conspecific worker, has acquired, somewhat in conformity to her increased bulk, a supplementary number of hamuli.

We return to Rayment's paragraph cited at the beginning of this section and wonder whether the "wing-hooklets" can indeed in all cases be regarded "as an infallible guide to the 'air range' of the bee," or whether greater weight of body does not to a certain extent nullify what seems a more favorable wing equipment. The lesser number of hamuli in *Trigona* as compared with *Melipona* has not prevented *Trigona* from spreading over the tropical regions of two hemispheres while *Melipona* is confined to the tropics of the

New World. Of course, many other factors are more important to survival and extension of territory than the ability to get around, but at least *Trigona* does not seem to have suffered from its supposed limitations of flight. Again, if number of hamuli are correlated with range of foraging, why has nature been so prodigal in the case of the bumblebee queen, who, it is true, forages for the first brood but subsequently is concerned with the indoor activities of her nest? And if flight range is progressive with the number of hamuli, are we to suppose that a queen of the large South American *Bombus dahlbomi*, which has an average of nearly 30 hamuli, has a flight range of around 10 miles compared to the seven miles attained by the honeybee with her average of under 21 hamuli? And what of *Psithyrus* that gathers no stores herself but lives, a parasite, in the nests of industrious bumblebees? Many of the females of that genus have an equipment of hamuli averaging higher than that of the honeybee worker. Here indeed would seem a waste of flight equipment upon an insect that has become a homebody.

Rayment's statement is intriguing, but it

would seem that experimentation in the field is needed on a large scale before his conclusion can be accepted without qualification. The weight of the insect, I am tempted to believe, is a factor that in many cases governs the number of hamuli, with the implication that a heavy insect with abundant equipment of wing hooks may have no greater flight range than a smaller insect with proportionately reduced number of hamuli. What is of particular interest, it seems to me, is the evidence that, in those genera of bees where the queen has become a mere instrument of egg laying, the royal caste tends to have fewer hamuli than the associated worker, whereas in communities where the queen still forages (at least in the incipency of the insect state) the supply of hamuli is abundant. In the case of *Psithyrus* it would seem that, although degeneration of structure has taken place in certain of the body parts, it has not yet affected the wing equipment. At any rate, *Psithyrus*, notwithstanding its present largely indoor existence, gives evidence of retaining the wing armature of what was probably a more enterprising period in its past, before dependence robbed it of initiative.

PRODUCTS OF THE STINGLESS BEES AND APICULTURE

HONEY AND ITS USES

Although insects and man stand at opposite poles both in their structure and in their behavior, the one representing possibly the highest development of instinct and the other, we like to think, the embodiment of reason, man is dependent on insects to an inordinate extent for his welfare and his very existence. No insects of the many that have served his needs have had a more indispensable part than the bees. Allusion has been previously made to the floral visits of stingless bees (p. 103) and the part they have in causing plants to set seed. This service transcends in importance all other services performed. However, when we think of bees we almost inevitably think also of honey and of wax, which are valued by man, and both of these are products not only of the honeybee but also of stingless bees.

Before the planting of sugar cane in the New World offered a challenge to the su-

premacy of honey as the source of supply for those craving sweets (and this period embraces the whole pre-Columbian era), the chief reliance of those living in this half of the world was the stingless bee, for the honeybee was introduced into this hemisphere only after the coming of the white man.

Columbus himself made early acquaintance with the native product. On his very first voyage he landed on Cuba, which he referred to as Juana, and there he noted among the natural assets of the island "a variety of honey" that with virtual certainty was that of *Melipona beecheii* variety *fulvipes* Guérin, as no stingless bee other than this one occurs in Cuba. The mention of this honey was made by Columbus eight months after he was sent by the King of Spain to discover a short route to the Indies and was addressed to "the magnificent lord, Raphael Sanxis, treasurer of the most illustrious king." It was "translated from the Spanish language

into Latin, on the third of the Kalend of May, 1493 by the noble and learned Leander de Cosco" and centuries later (1892) was republished by the Lenox Library, New York (1946, Encore, pp. 354-360). The first mammal mentioned by Columbus in the narrative of his discoveries was the Caribbean seal, and the first plant he noted was tobacco. The first insect product with which the Admiral of the Ocean Sea became acquainted in the New World was apparently honey and it could only have been the honey of a stingless bee.

In all probability the honey observed by Columbus in Cuba was wild honey, but in nearby Yucatan apiculture has had a long history. Gómara (1578, p. 200) indicated that honey was an article of sale in the great market place in Mexico City at the time of the Conquest and there were "sundry kinds." In Central America and South America, too, the natives were aware of its palatable appeal. To this day the honey of stingless bees is relished widely throughout the tropics of the New World and the Old, and a survey of its quality and its uses seems in order.

A peculiarity of the honey of stingless bees is that it usually resists crystallization, often remaining in a fluid state indefinitely. More than a century and a half ago Fermin (1769, p. 301) commented on the continuous liquidity of the native honey. Goldsmith (1824, p. 146) affirmed that it "never congeals, but is fluid." Peckolt, who made analyses of the content and quality of the honey of a number of the stingless bees, affirmed that it fails to crystallize even when kept for a long period. As quoted by H. von Ihering (1903, p. 267), Peckolt claimed to have had stingless-bee honey in jars which after 30 years still failed to show any crystallized sediment, a condition which Peckolt contrasted with that shown by honey of *Apis* even after only a few months. However, not invariably does the honey of stingless bees resist this change. According to Bertoni (1911, p. 143) the honey of *Trigona* (*Tetragona*) *jaty* F. Smith undergoes crystallization in winter in Paraguay, and H. von Ihering (1903, p. 270) commented that not only in a nest of *jaty* but also in a nest of *Melipona marginata* Lepeletier he had come upon honey jars that contained virtu-

ally only loose bits of light crumbling white sugar instead of the fluid honey.

The honey of various stingless bees tends to degenerate sooner or later even if it does not crystallize. Fermin noted long ago (1769, p. 301) that it easily turns sour. In winter the usually sweet honey of *Trigona* (*Plebeia*) *mosquito* F. Smith turns acid and at times suffers an albuminous fermentation (Bertoni, 1911, p. 145). Of the honey produced by the bee popularly known as "mumbuco," probably *Trigona* (*Cephalotrigona*) *capitata* F. Smith, it is stated by Gardner (1846, p. 328) that after being kept about an hour it "becomes sour as lemon juice."

Yet it is not to be inferred that in all cases is degeneration rapid. Peckolt (1894, p. 90) spoke of having preserved for 20 years the honey allegedly of the very same bee (Peckolt called it "mombuca") denounced by Gardner. Even after that long lapse of time the honey, although somewhat sour, was still pleasant to the taste and without dregs. The honey of *Melipona beecheii* variety *fulvipes* Guérin seems to maintain its quality. F. Poey (1852, p. 159) stated that he had kept the honey of this bee for an entire year, without any artificial aid, in flasks that were poorly plugged. Yet it had not fermented. Even sour honey might have its uses. Kidder and Fletcher (1857, pp. 454-455), after stating that some of the Brazilian stingless bees make sour honey, add that it "will compensate for sweet lemons."

Boiling of honey reduces its sourness according to "a man of Piste" in Yucatan cited by Redfield and Villa R. (1934, p. 50). In the sixteenth century Bishop Landa (1941, p. 194) pointed out that the honey of stingless bees in Yucatan "sometimes comes out a little watery and it is necessary to give it a boiling, and when this is done it is very good and keeps very well." According to H. von Ihering (1903, p. 270), the honey of stingless bees, usually very fluid, is cooked throughout Brazil until it acquires the desired degree of thickness, and this author went on to state that without such a preparation the honey could be preserved for only a short time. Guenther, too, confirmed the fact (1931, p. 298) that boiling of honey is usual in Brazil. Possibly such treatment as well as the quality

of the honey itself may explain the relatively greater resistance to degeneration in certain cases than in others.

To make the honey more fluid rather than less so was sometimes the goal. A favorite way of serving honey was, and apparently still is, to mix it with water (Marcgravius, 1648, p. 259; 1942, p. 259; Wied Neuwied, 1820-1821, p. 247; Tessmann, 1930, p. 371). Not infrequently this combination is permitted to ferment, resulting in a slightly intoxicating drink (Azara, 1809, p. 161; Nordenskiöld, 1929a, p. 170; 1930, p. 197).

Not infrequently, however, more than a mildly intoxicated effect was experienced. The eighteenth century Jesuit missionary, Florián Paucke (1942, p. 95), who served his order during 18 years in Paraguay, stated that especially from the beginning of November onward when the heat was intense, the Indians were accustomed to make a drink of honey and fruits which they consumed by day and by night, waking from their drunken slumber only to indulge again. On these drinking bouts there would sometimes be assembled more than a hundred Indians. Always these parties ended in uncontrolled demonstrations of violence, so that the women took the precaution while their husbands were drunk to conceal all weapons in order that upon emerging from their stupor the men might have only their bare fists with which to inflict damage on one another. According to Azara a honey produced by one of the seven stingless bees known to him from Paraguay caused violent headaches and was "as intoxicating as aqua vita." Possibly it is the same honey alluded to by Paucke in the passage just summarized, although that author indicated later (1943, pp. 197-198), that more than one type of potent honey was employed by the Indians, including that of wasps as well as of bees.

In another connection Paucke gave an account of the way the intoxicating drink was prepared. Little work and refinement were needed, Paucke indicated (1943, p. 198), for the accomplishment of the task. The Indians took a raw and dried hide of a jaguar or of a deer, which they suspended in such a way that it formed a pouch. Into it they dumped the honey as well as the wax, poured water

upon these, and left the mixture to ferment under the heat of the sun. In three or four days the brew thus exposed attained the desired degree of potency. To designated tasters was assigned the responsibility of testing the progress of the brew and determining whether it had the right strength. When the tasters pronounced the beverage as fit to drink, the summons went forth to the most distinguished. Those who were not yet qualified to be participants in the actual drinking bout were, nevertheless, permitted to attend in a capacity somewhat resembling that of a cupbearer. Those denied the right to drink included young men and bachelors, unless they happened to be sons of a cacique.

Nieuhoff (1813, p. 733), who sojourned in Brazil from 1640 to 1649, spoke of a small native bee that he designated "thanbuka," which produced an aromatic honey. Of this honey the inhabitants made "metheglin, which is very strong, and will keep a great while." Also, according to this author, you could "make meath of this honey without boiling, only mixed with some spring water, and exposed to the weather." Metheglin, the dictionary defines as "a beverage usually made of fermented honey and water." That other ingredients might at times be added is indicated, however, by the fact that Queen Elizabeth of England, who died less than 40 years before Nieuhoff visited Brazil, was partial to a metheglin in which not only were there equal quantities of water and of honey—a gallon of one matching a gallon of the other, beaten up together "for the space of an hour"—but also such flavoring elements as a "bushel of sweet briar leaves, as much of thyme, and a peck of bay leaves." In addition ale or beer were required for the proper completion of this royal drink (cited by Ransome, 1937, p. 200, from "England's interest," 1707, by Sir John More). It is unlikely, however, that the metheglin drunk in Brazil underwent so many refinements in the course of its preparation. The indication that the brew of "meath" could be achieved merely by the addition of water and by exposure to the weather is reminiscent of the technique cited in the previous paragraph.

In the Old World, as in the New, honey of stingless bees was sometimes diluted with

water and served as a beverage. This is the way that honey that has become ingrained with grit is almost invariably served by the aborigines of the north coast of Australia (Basedow, 1925, p. 153).

In São Paulo, Brazil, according to H. von Ihering (1903, p. 272), the honey of a *Trigona* called "feiticeira" ("enchantress") or "vamos-nos-embora" ("let us be off") has the reputation of being extraordinarily intoxicating. According to folk tale he is destined to die who after taking this honey invites his friends to break up their meeting, but others say that the popular name "vamos-nos-embora" is derived from the fact that those partaking of the honey become too intoxicated to find their way out of the forest. The bee on which these names have been bestowed is here interpreted very doubtfully as *Trigona* (*Trigona*) *recurva* F. Smith. The reader is referred to the account of that species on a later page of this book (p. 228) for fuller elucidation.

According to Spegazzini (1909, p. 40) the honey of what he referred to as *mombuca* is agreeable to the taste but produces an intoxicating effect due, he believed, to the fact that the bees in their foraging frequent flowers of narcotic properties. Spegazzini had this inebriating experience in Misiones, Argentina. The bee was probably not the species that F. Smith described as *mombuca* but possibly the same author's *capitata*, a popular name of which is "mombuca."

Scooping out a felled tree until it served as a trough, the Chiquitos Indians of South America would submerge therein the wax they had gathered in order to free it of adhering honey. Then, adding more honey and allowing the mixture to ferment, they would

produce a drink called "guarapo," which D'Orbigny (1839-1843, p. 615) found very palatable. This drink constituted their main and (except for a few ears of corn) their sole diet while off on honey gathering and wax collecting expeditions.

The seventeenth century Carmelite friar, Vázquez de Espinosa (1942, p. 685), stated that wine was made from honey by the Guarcurús, described (p. 683) as "a degenerate and indolent people" that "neither sow nor reap." This honey wine the Guarcurús used in a drinking ceremonial that was celebrated whenever their cacique died. On such occasions, when exhausted and inebriated by the orgy, the bravest of the warriors asked others to choke them to death so that they might accompany their leader. When this unnatural request was fulfilled, the dead warriors were placed at the side of their chief, with an equal number of slain boys at their feet, and weapons, food, and drink to sustain them on their journey. Then the vault or cave holding this company of the dead was covered over, and those surviving this gruesome rite dispersed.

According to Storm (1945, p. 347), "Merry-making in antique Michoacán required charapi, as they do today. This drink whose base is honey belongs to the region as tepache belongs to Mexico."

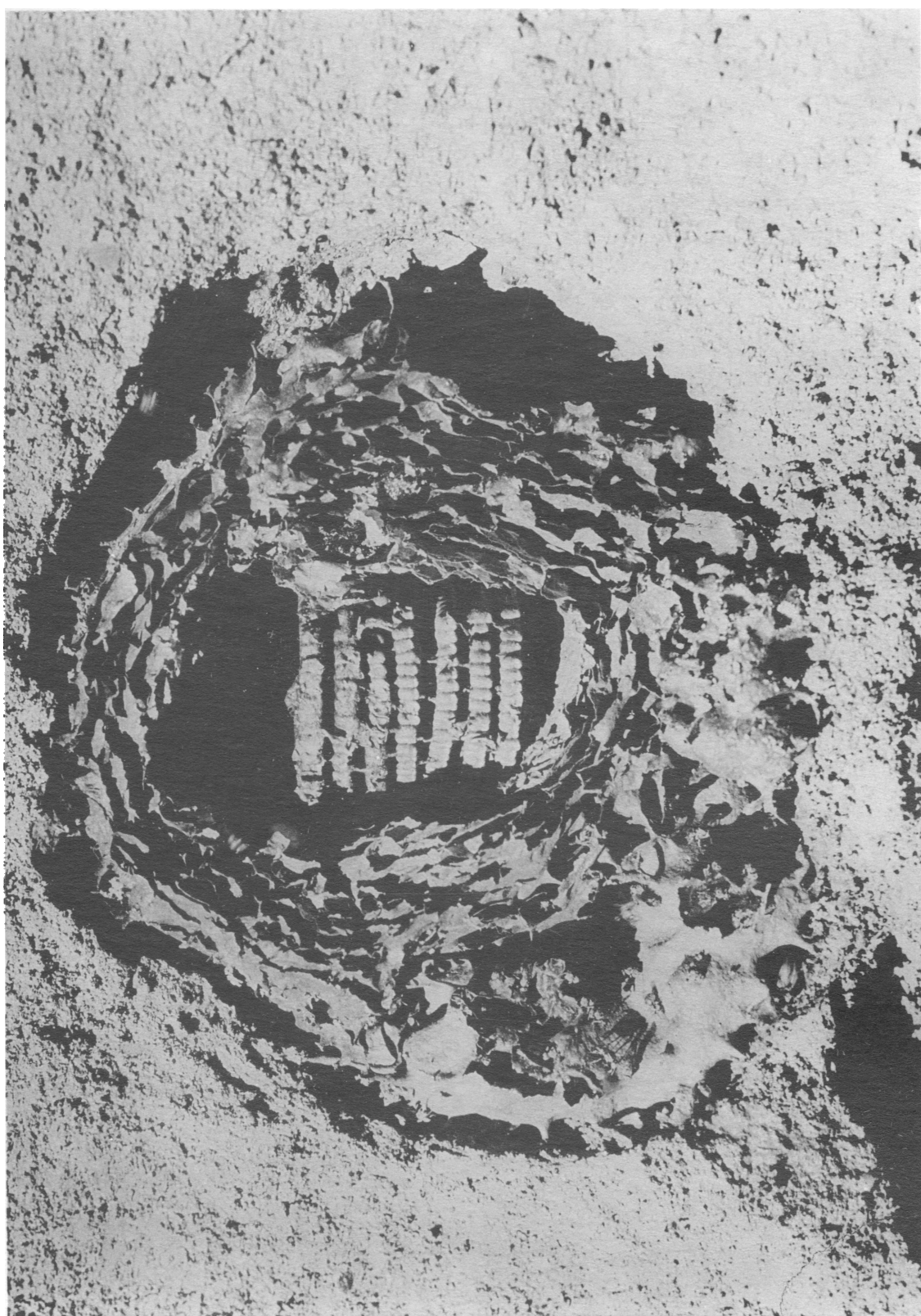
Among the Chorti Indians of Guatemala a sucrose wine, known as "chicha," is prepared in various ways. One of the methods is to use as ingredients corn and honey. "Chicha," it is said, is the only intoxicating beverage made by the Chorti, and great quantities of it are consumed on all ceremonial and festival occasions, every family keeping a supply in

PLATE 7

Nest of *Trigona* (*Paratrigona*) *lineata* variety *nuda* Schwarz, erected in a deserted fungus chamber of the fungus raising ant, *Atta sexdens*. There are seven brood combs, with a width of about 5 cm., surrounded by the labyrinthine involucre. The three top combs contained, according to W. Weyrauch, who took the photograph, only nutrient and eggs; the four lower combs had pupae. The nest is from 11 cm. to 14 cm. in diameter. The involucre consists of numerous layers. The length of the cells is 4.5 mm., their width 2.45 mm. In the lower part of the nest are the honey pots,

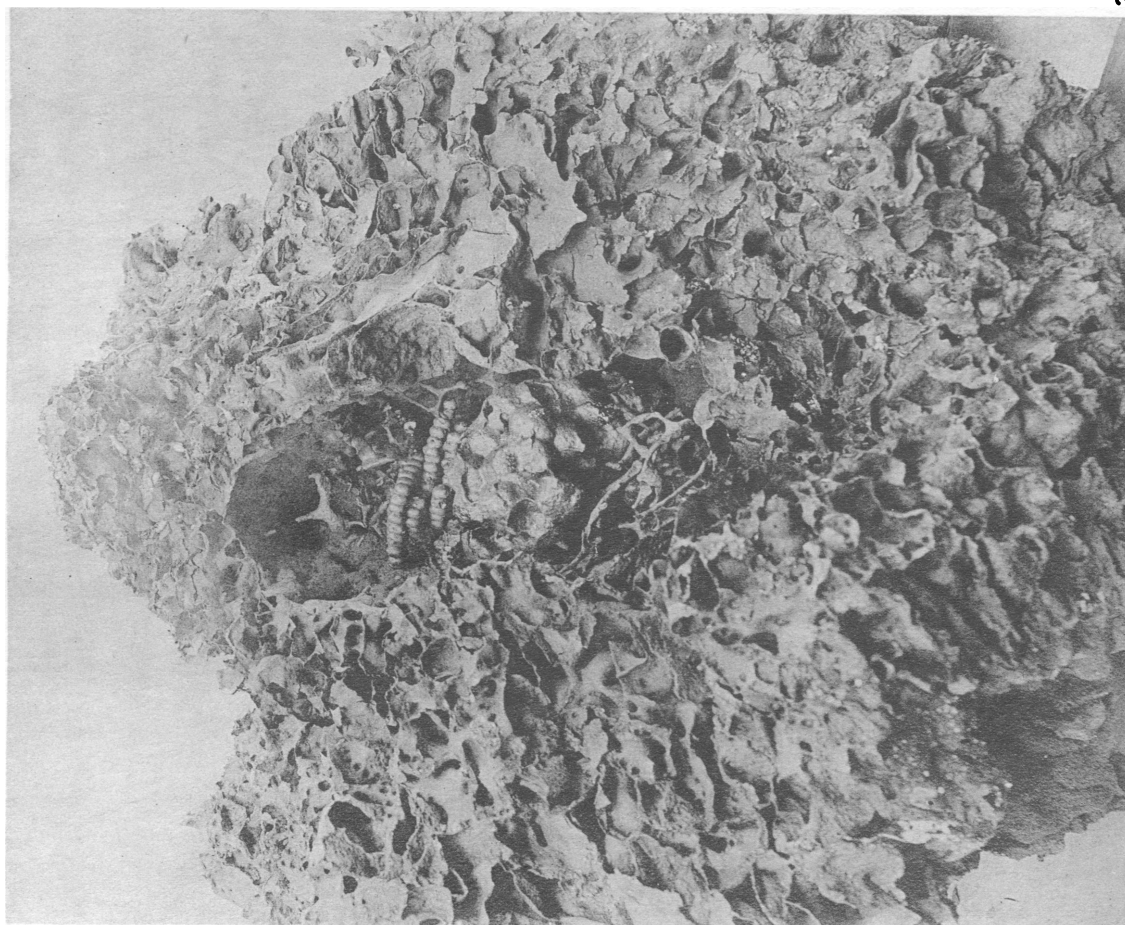
and the dark space immediately below the nest at the left is a more or less destroyed connecting passageway of the ants.

Stingless bees not infrequently adopt as their place of residence hollows that have been previously excavated by other creatures. It is not unlikely that the cavities in trees, which are favorite nesting sites, are started in certain cases by tree infesting beetles. Termite nests are places chosen by certain stingless bees, and even the nests of birds are sometimes occupied. In other cases stingless bees live, as here indicated, in ant nests.





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reserve for such indulgence (Wisdom, 1940, p. 105).

A drink known as "sac-ha" is prepared in Yucatan. Its ingredients, according to E. H. Thompson (1932, p. 62), are "corn in the milk and wild honey." After a picturesque ceremony dedicated to the rain god, in which there was much consumption of "balché" by the men, the women were permitted to partake not of the "balché" but of "sac-ha."

"Balché," in which honey was an ingredient, was the ceremonial drink of the Maya of Yucatan, and drunkenness was compulsory in certain of the religious rituals. The degree to which those participating complied with this mandate is illustrated by the statement of Landa (1941, p. 91) that "they made wineskins of themselves." It has seemed best to postpone a fuller account of "balché" until a later section of this Introduction. Here mention may be made, however, of the fact that, while it is still employed on ceremonial occasions by the Lacandon of Chiapas and by the Maya in Yucatan (Tozzer, 1941, p. 198), and also in the Toledo and Corozal districts in British Honduras, its use has been discontinued in the Socotz district of the latter country (J. E. Thompson, 1930, p. 104).

Another drink of the Maya (referred to as a "very refreshing drink") was "keyem," known to the Spanish and Mexicans as "posole." For the preparation of this beverage, Indian corn was hulled by boiling with lime. Thereupon, it was washed with care and ground into a paste, which in turn was

mixed with water sweetened with honey (E. H. Thompson, 1932, p. 43).

In Yucatan, honey figured not only as an ingredient in drinks but was used also as a food. Roys (1943, p. 42) stated that a sweet dish composed of toasted squash seeds and honey is still popular in that peninsula, and that a dish of parched corn and honey is mentioned in "The book of Chilam Balam" of Chumayel.

The Chorti Indians of Guatemala sometimes boil honey with foods as well as drinks, but as a rule they sell it in the market, where it is offered in small pitchers and bottles (Wisdom, 1940, p. 69).

Strange culinary uses were found for honey in South America. Fish was made more palatable to the inhabitants of Sertão in southern Brazil when seasoned with honey (Saint-Hilaire, 1830, pp. 370-375). Honey mixed with farina seems a less incongruous combination. It was thus prepared in the State of Goyaz, Brazil, according to Gardner (1846, p. 329). Potatoes also were eaten with honey (Paucke, 1944, p. 189).

Various medicinal virtues were attributed to the honey of stingless bees and hence it was much prized by pharmaceutical establishments. As far back at least as the middle of the eighteenth century apothecaries of Surinam offered it among their wares (Fermin, 1769, p. 301). Apparently the supply of native honey often fell short of the demand for it, whether owing to lack of enterprise on the part of the inhabitants in gathering it or to

PLATE 8

Nest of *Trigona* (*Paratrigona*) *impunctata* (Ducke) erected within the structure of a termite, *Nasutitermes* (*N.*) *similis* Emerson.

1. The nest in detail.
2. The brood combs and the provision containers below the combs.

Emerson's description of the nest reads: "Small compartment with smooth interior. Combs in three layers and honey cells under it. All was supported by wax filament structure." The brood cells measured 2.25 by 4 mm. Notwithstanding the occupation of the termite colony by the bees, the activities of the termites went on apparently unhindered. The colony was a populous one and from it Emerson collected "the king, queen, workers, and soldiers as well as Staphylinid termitophiles."

Photographs by Alfred Emerson.

Most species of stingless bees have never been observed to nest in colonies of termites. A few species of adaptable nest habit occasionally are found using such nests as a homestead. This may even become the predominant habit of a species in a given area, as reported by Nevermann for *Trigona* (*Trigona*) *amalthaea* (Olivier) in the San José region of Costa Rica. In other cases, notably in the case of *Trigona* (*Scaura*) *latitarsis* Friese, the termitophile habit is invariable or almost invariable. One suspects this may be the case also for *Trigona* (*Paratrigona*) *impunctata* (Ducke), the few known nests of this species and of the closely related *isopterophila* having all been located in termite structures.

other deterrent reasons. At any rate, Voisin, writing from French Guiana in the third quarter of the nineteenth century, complained that, although that colony was in a position to supply the mother country with excellent honey, it expected, instead, to have its own needs supplied. Imported honey was sold in the apothecary shops of Cayenne, but it was recorded as being very costly (Voisin, 1873, p. 260). On the other hand, in southern Brazil, bottled honey of stingless bees that was sold to apothecaries commanded a price four or five times that of the honey of *Apis mellifera* (H. von Ihering, 1903, p. 274). Such a disparate price points not only to the inordinate faith of the purchaser in the curative helpfulness of the honey of stingless bees but also to the inadequacy of the supply. Indeed, Koster (1816, p. 319) indicated in his account of conditions in the State of Pernambuco, Brazil, during the early years of the nineteenth century that the limited quantity of honey available there was devoted to medical purposes with the virtual exclusion of its use as a food. From another state of Brazil, namely, Minas Gerais, Saint Hilaire reported (1830, p. 371) that the inhabitants placed considerable reliance in the curative aid of the honey of stingless bees, and Hannemann indicated (1872, p. 207) that in Paraguay, too, it was offered for sale in the drug stores.

What, then, were the special medical applications and uses of honey? It was deemed of aid for nasal, throat, and pulmonary ailments. Father Labat, who traveled in French Guiana in the middle twenties of the eighteenth century, stated (1730, p. 265) that in that country honey of stingless bees was used as a remedy for colds and what he described as "dryness of the chest," and, writing nearly two centuries later, H. von Ihering could report (1903, p. 273) that the native honey was still a favorite remedy in southern Brazil for the cure of consumption.

The honey of specific bees was supposed to have value for specific ailments. Honey of *Trigona basalis*, a synonym of *Trigona (Schwarziana) quadripunctata* variety *bi-partita* (Lepeletier), was, according to Peckolt (1894, p. 90), a popular remedy for catarrhal infections in southern Brazil. That of *Trigona (Tetragona) jaty* F. Smith is similarly said to have curative properties for those suffering

from a sore throat (Jacob, 1932, p. 149). In addition the claim is made that the honey of *jaty* has potency in the cure of ophthalmias and likewise ailments of the lungs (Marianno, 1911, p. 111). Several writers, including von Spix and von Martius (1828, p. 524), pay tribute to the delicious quality of the honey of *jaty*; evidently there is no need for sugar-coating this acceptable remedy. A folk use for the honey of a subterranean species known in southern Brazil as "abelha do cachorro do chao" was in stopping blood flow (Peckolt, 1894, p. 225), and Anchieta, writing about the same region much earlier (1812, p. 155), mentioned the use of honey in healing wounds, which, the good padre assures us, was achieved easily with God's help.

Some honey is strongly aperient (Marshall, 1898, p. 132; Nordenskiöld, 1929a, p. 170, and 1930, p. 198) and is used as a remedy for constipation (Drory, 1872b, p. 158). According to Peckolt (1894, p. 90) a bee he designated *mellea* is known in Brazil as "cutiã da purga" because the honey is given to children as a purgative. The brief description that Peckolt gave of this bee makes it almost certain that it was not *mellea*, which is itself a synonym of *Trigona (Trigona) pallida* (Latreille).

A quaint seventeenth century account of the aid to digestion of stingless bee honey is communicated by "Mr. I" (Villermont, 1685, pp. 1030-1031): "My Friend (a Monsieur de Villermont) tells me, he thinks, the liquor [the honey] is one of the most agreeable things in the world. If you drink fasting, the quantity of a good Glass, or about half a pint, it will give you 2 or 3 stools, in about 2 hours time, according to the temperament of the Party; but if you drink it at Meals, it does not purge at all." Nieuhoff (1813, p. 733) spoke of the honey of the Brazilian bee known as "thanbuka," previously mentioned, which, of an agreeable odor, "is accounted very balsamic, corrects the sharp humours in the intestines, and especially in the kidneys, and provokes urine." Evidently the honey of "thanbuka" was valued not only as a main ingredient of metheglin but also medicinally.

It is difficult to decide to what extent the medicinal virtues claimed for the honey of stingless bees are validated by an improvement of the patient that is traceable to the

consumption or application of the honey. It would seem that in many instances the use of the honey may have been governed by folk custom. Imitative magic rather than medical experience certainly underlay some of the prescriptions in which honey was an ingredient. Notably fantastic, not to say repulsive, are the remedies that figure in the pharmacopoeia of the Maya, of which many are here cited from the interesting volume, "The ethno-botany of the Maya," by Ralph L. Roys. In prescribing some of these medicines, in which honey is frequently the only palatable element, the "ah-men" must have contributed not seldom to the misery of his patient without effecting the promised cure.

Mention has been made of imitative magic. Unmistakably suggesting imitative magic is the following Maya prescription: "For blood-vomit which is very red in a man, the leaf of the *Colubrina Greggii*, Wats., the leaf of the *Bixa orellana*, L. (*Achiote*), the *Tubiflora squamosa* (Jacq.), Kuntze, their tubers and their roots together, and the red part of the *Gouania domingensis*, L., and the red bole employed by a painter for gilding, and the red *cuxum-che* (mouldy tree). This is round; this is very red. Also very red old ripe chile and the juice of lemons, the liquid or juice of the *taa-tzimin* (horse dung or tapir dung), this *castaño* (chestnut), and the *Dorstenia contrajerva* L. (*Contrayerba*), and virgin honey, fresh from the hive" (Roys, 1931, p. 64). One has had to wait till the end for mention of honey in this array of ingredients evidently selected because their color resembled that of the bloody discharge.

"Bloody vomit" was, however, only one of many ailments that the Maya claimed to be able to cure with the aid of honey. A bloody flux, possibly dysentery, was stopped by inducing the patient to drink a brew concocted of a handful of lemon leaves, the leaf of *Bursera simaruba* and that of *Diphysa robinoides*, and approximately one-third of a drachm of honey, fresh from the hive (Roys, 1931, p. 39). This, as Maya remedies go, does not seem too uninviting, but one stands somewhat aghast at one of the drastic cures for blood in the feces, namely, a mixture in which the ingredients are "a little gunpowder," the yoke of an egg, and a small quantity of honey beaten up with a little

water and some *Myrtus pimenta* (Roys, 1931, p. 58).

The ear, eye, and throat division of Maya medicine relied on honey. If the throat was swollen, *Solanum nigrum* with a little honey was to be applied lightly (Roys, 1931, p. 192). Honey, as hot as the patient could stand it, along with tobacco, was used in a poultice applied to those suffering from loss of speech, presumably epilepsy (Roys, 1931, p. 87). Not only the organ of speech but that of hearing as well was benefited by honey. One of several prescriptions for ear-ache was to drop into the ear honey that had been steamed over hot ashes in an old ripe red chile from which the seeds had been removed. If this remedy failed, a boy's urine prepared in precisely the same manner was to be substituted for the honey (Roys, 1931, p. 94). It was the belief that eye soreness, too, could be relieved by boiling honey with tender tips of *Carica papaya* under a covering of banana leaves, not forgetting to add a little salt, and then squeezing the resulting blend into the eye (Roys, 1931, p. 100).

A miscellaneous lot of ailments, related for the most part only through the fact that they appeared as eruptions or discolorations of the skin, were treated with honey by the Maya. To cure jaundice and biliousness honey was given the patient on nine occasions at dawn in a drink that included the boiled leaf of *Capraia biflora* Linnaeus (Roys, 1931, p. 128). Honey fresh from the hive was an ingredient in a drink intended to cure an eruption of livid spots (Roys, 1931, p. 73). A disease described as "black confluent smallpox" was treated by having the patient swallow a beverage consisting of honey mixed with the roasted and mashed blossom, leaf, and outside of *Plumeria rubra*, all heated to just the right temperature (Roys, 1931, p. 146). Not roasted but the raw, crushed leaves of several different plants in fluid honey was a prescription believed to contribute to the relief of "a contagious eruption that comes to a man's head" and the throbbing of which descends from the head down to the heart (Roys, 1931, p. 147). A mixture of salt, oil, and honey held in the mouth was supposed to reduce a swelling on the tip of a sore tongue (Roys, 1931, p. 132). Honey strained through a cloth or handkerchief was an ingredient in a

complicated prescription, with many alternatives, that was guaranteed to cure scrofulous tumor of the neck (Roys, 1931, p. 177).

Hiccoughs, it was claimed, would disappear if honey fresh from the hive, followed by hot water, were given to a sufferer, but recovery was not promised in cases described as "fatal hiccoughs" (Roys, 1931, p. 116).

To cure pain in the heart, the Maya recommended that there be applied to that organ a cloth on which had been placed honey burned with roasted anise and mixed with wine (Roys, 1931, p. 35).

Ailments that were the result of accidents were also relieved by ministrations of honey combined with other incongruous things. The blood from "a large fowl with a back like that of an owl and feathers like a turkey" heated and then mixed with honey was to be consumed by anyone who had been bitten by a snake or by a mad dog (Roys, 1931, p. 25). In the case of a burn, honey fresh from the hive was to be applied immediately (Roys, 1931, p. 68). Honey was also deemed curative for pain caused by sorcery (Roys, 1931, p. 207).

Like the Maya, the Chorti Indians of Guatemala also included honey in their *materia medica*. If a person suffered a body blow, the honey of a small wild stingless bee, known locally as "talnete," was drunk in order to relieve the pain and swelling, and this honey was applied, also, to a sensitive area of the body (Wisdom, 1940, p. 360).

With the Maya, a remedy for retention of urine included, in addition to honey and wine and the plant *Guazuma ulmifolia*, such unsavory ingredients as ox dung, horse dung, and garlic, all of which were to be boiled together (Roys, 1931, p. 197). Honey also figured in one of the prescribed remedies for pus in the urine (Roys, 1931, p. 200).

Honey was an ingredient in some of the fantastic medicines used by the Maya for the supposed benefit of sick children. A concoction consisting of the leaves of various specified plants crushed raw in a given quantity of honey was a remedy devised by the Maya for boys suffering from what is designated "knife-thrust diarrhea," and those administering it are cautioned to induce their young patients to persist in drinking it even though they vomit or are afflicted by cramps (Roys, 1931, p. 53). Mr. Arthur Carpenter,

who made an extensive sojourn at Lake Izabal, Guatemala, tells me that the natives of that region use the honey of stingless bees not only for dysentery but for throat soreness and for all sorts of ailments affecting children.

Those suffering from dry cough, asthma, and whooping cough were advised by the Maya to take the bark of the *Plumeria alba* Linnaeus, the plant known as the "flor de Mayo blanco," boil it with lemon juice or orange juice, add honey, and drink the concoction (consisting of four gourds of liquid) while it was tepid (Roys, 1931, p. 8). A leaf of a radish boiled with honey and vinegar was credited by the Maya with being a cure for what was probably a complicated case of pneumonia (Roys, 1931, p. 11). A remedy prescribed for consumption by the same people read: "Take a tomin of honey and half an ounce of Spanish pepper. Grind it and sprinkle it on the honey. Also twelve chile peppers and half a leaf of tobacco, pulverized, also. Then let it be put in the honey and boiled until it has boiled away. If there is a chill, you take it cold and put it on the end of his tongue until it is sucked away. Then let him cover himself up and not drink cold water for three days. With this he will recover" (Roys, 1931, p. 12). A disposition to spit incessantly was controlled by swallowing, steaming hot, a drink consisting of boiled *Euphorbia hirta* Linnaeus or some other small prostrate *Euphorbia* to which honey had been added (Roys, 1931, p. 131).

This section is devoted to honey and its uses, yet it may be in order to inquire in passing whether the producers of the honey were assigned therapeutic value. Wasps and wasp nests contributed their potency to several medicines devised by the Maya. Bees are more rarely an ingredient. However, in a medicine intended for the cure of an unidentified disease designated deer-spasm there were included the nest of the "kukliz-cab" (interpreted as a variety of bee) to the inclusion of the old insects as well as the young ones, the "ah-muul" (said to be "a variety of wasp with yellow-tipped wings which makes its nest underground"), and the larvae of the "ah-choch" (a variety of bee). These were to be crushed and mixed with burned deer horn and then offered to the patient as a drink (Roys, 1931, p. 206).

While the Chorti Indians of Guatemala may not use the larvae of stingless bees as ingredients of their remedies, the medicine man nevertheless relies on immature bees (probably larval stingless bees) to prove his ability to extract worms from their fastnesses within the patient's anatomy. After first addressing threatening remarks to the worms, he engages in a pulling motion just above the patient's head and nose, claiming thereby to force all the worms out of the rest of the body into the head and thence through the nose. Then by deft finger action he manages at the significant moment to slip into a gourd, held near the patient's nose, the bee larvae that he has gathered for the purpose, and thus convinces the credulous that he has succeeded in extracting the worms that were responsible for the ailment (Wisdom, 1940, pp. 350-351).

In the State of Guerrero, Mexico, honey of stingless bees is regarded as being efficacious in the cure of certain stomach ailments (Hendrichs, 1941, p. 372). Among the Popoluca Indians of Vera Cruz, Mexico, the common use for the honey of the stingless bee known locally as "abeja real" (probably *Melipona beecheii* Bennett), is as an unguent on wounds, cracked lips, and various infections of the skin (Foster, 1942, p. 539).

At the Maya village of Chan Kom, honey is given to mothers after childbirth (Redfield and Villa R., 1934, p. 49). Similarly among the Maya Indians of east central Quintana Roo, an area in the eastern section of the peninsula of Yucatan, Mexico, honey sweetens the chocolate that is drunk by a woman after the birth of her child (Villa R., 1945, p. 58).

A Maya prescription affecting the after-birth is worthy of being quoted in full because of the odd assortment of ingredients in addition to honey that are cited: "The remedy is a medio of honey heated with a little sugar, not much, roasted, powdered and stirred thoroughly into the hot honey. Let it be given to drink to the patient. It will be good to put immediately the blood of a chicken in it, the blood from the leg of the chicken. (When for) two days the after-birth may be retarded in part, administer the other remedy for the after-birth, grated *Jatropha aconitifolia*, Mill. (*Chaya*) with horse-dung and honey and *Capsicum annuum*, L. Let

it be drunk warm" (Roys, 1931, p. 17).

To bring on parturition in a woman the Maya had two methods, both involving the use of honey. One took mint, mashed it with water and honey, and then administered it to the patient, whereupon, the assurance is given, "immediately she will be delivered." An alternative remedy was to take honey and oil and burn them under the patient, as a result of which instant delivery was promised (Roys, 1931, p. 20).

On the other hand, among the Akamba of Kenya Colony, east Africa, honey was withheld from women during pregnancy in the belief that partaking of it would be injurious to the unborn child (Thorp, 1943, p. 259) or to the mother owing to the fact that the honey causes the child to grow inordinately and so makes delivery more difficult (Lindblom, 1920, p. 29).

Honey is added by the Maya of east central Quintana Roo to the holy loaves known as "oxdias" and to the ceremonial drink designated "caliz" (Villa R., 1945, p. 58).

In Chan Kom, a Maya village, many foods were classified as "hot" or "cold" quite irrespective of their actual temperature. Honey was interpreted as a very hot food (Roys, 1943, p. 93), but its heat might be more or less neutralized if to it was added some food believed to be cold. Foods that were thought of as cold included "peccary, wild turkey, rice, boiled eggs, limes, lima beans, pork, Jícama, squash, lard, two bananas known as x-box-haaz and bárbaro-haaz, the meat of the large deer and all foods cooked in an earth-oven." On the other hand, coffee, a beverage likewise interpreted as very hot, was intensified in hotness if honey was added to it. Hot and cold foods had their medicinal uses. A person suffering from a fever would avoid taking ingredients interpreted as hot, although in some instances a hot food like honey was actually prescribed with other ingredients for fever patients.

For instance, a concoction made from the root of *Triumfetta semitriloba* Linnaeus mashed in honey was deemed of aid to a Maya patient suffering from a fever unaccompanied by perspiration. The remedy was to be taken not only internally but externally, too. "Let it be anointed all over the body"

is the direction; "cover him up so he will perspire, for a remedy" (Roys, 1931, p. 74). Here one is inclined to infer that the inclusion of honey in the prescription was precisely because a "hot" substance was required to induce sweating.

Honey was an ingredient, too, in a drink offered a child afflicted with convulsions and chills (Roys, 1931, p. 76), doubtless because of its heat imparting quality as interpreted by the Maya, and it figured likewise in a remedy for recurrent chills that had as another ingredient the urine of a boy ("as much as a large gourd full") in which were to be boiled the leaf of *Urera microcarpa*, a leaf of green tobacco, the leaf of *Sinapis niger*, a handful of *Helenium quadridentatum*, a handful of the leaf of *Pluchea odorata*, the leaf of the orange tree, a little lard, and a handful of salt. This remedy was to be applied externally (Roys, 1931, p. 77).

A Maya Indian suffering from a chill or weakened by illness was cautioned to eschew cold food. Cold foods, it was believed, required further cooking in the body and hence the morning was the time to partake of such foods, because it allowed a longer interval for the completion of the internal culinary processes (Redfield and Villa R., 1934, pp. 161, 171).

It is in order to point out that, while the Maya denied the fever patient honey under the impression that as a hot substance it merely tended to raise his temperature, the Botocudo Indians of Brazil in complete reversal of such a belief were accustomed to administer honey in cases of high fever.

Among the Maya Indians of east central Quintana Roo, honey produced by bees known as "xiic" is used medicinally (Villa R., 1945, p. 58). This bee, sometimes spelled "xik," is, as I have indicated in a later connection (p. 148), probably *Trigona* (*Tetragona*) *nigra* variety *nigra* Cresson.

The honey of Old World *Trigona*, too, had its medicinal uses, real or fictitious, and in some cases, at least, was administered for the cure of ailments identical with those from which people suffered in the New World. The honey of the African *Trigona beccarii* Grubbe, mixed with a native flour, is reported by Morstatt (1921, p. 287) to be a remedy for coughs. Much prized by the African tribe

Wadschagga is the honey of *Trigona erythra* variety *togoensis* Stadelmann, which, in addition to its tastiness, has the virtue, it is claimed, of curing diarrhea and stomach and intestinal ailments, particularly those of small children (Morstatt, 1921, pp. 294-295). The delicious honey of another African stingless bee, the "moka" (presumably *Trigona clypeata* Friese), has, according to Marais (1912, p. 793), the reputation "of possessing many therapeutic properties, especially in certain female ailments, and is on that account greatly valued."

In contrast to honey that was deemed helpful were other types of honey that were definitely injurious. The honey of three kinds of stingless bees found in what is referred to as the Province of Chiquitos, Bolivia, was pronounced dangerous by D'Orbigny (1839-1843, pp. 616-617). The honey of two of these, known, respectively, as "oreceroch" and "overcepes," caused terrible illness; that of the third, "omocayoch," was delicious to the taste but inebriating as a drink of liquor, often causing temporary loss of reason. Some "detestable" honey produced by black bees that had their nest in the soil is mentioned by Saint-Hilaire (1848, p. 150). The vomiting that this honey occasioned was cured by drinking tea.

In the case of a bee like *Lestrimelitta limão* (F. Smith), which rather persistently produces poisonous honey, it would seem, possibly, that the toxic qualities of its products are due to the plants visited although its floral visits have not been recorded. (The reader is referred to the discussion of *Lestrimelitta*, p. 178, for fuller comment on the poisonous quality of the honey of *limão*.) Certain other Meliponidae produce sometimes wholesome, sometimes unwholesome honey. According to von Spix and von Martius (1828, p. 524), the inhabitants of Sertão in southern Brazil stated that this fluctuation was seasonal, depending on the blooming time of certain plants. F. Poey (1852, p. 159) was distinctly of the opinion that poisonous honey derived its toxic qualities from the plants visited by the bees, and this was the opinion also of Drory (1872b, p. 158).

It is in order to state that the unsanitary habits of many stingless bees may also possibly account for the unpleasant conse-

quences sometimes associated with the consumption of the honey of these bees. Thus Wheeler (1913, pp. 6, 7), in commenting on the partiality of *Trigona* (*Scaptotrigona*) *bipunctata* variety *wheeleri* Cockerell and of *Trigona* (*Trigona*) *corvina* Cockerell for visiting excrement and congregating in latrines, wondered whether the "baneful effects" sometimes the result of eating the honey might not be due to "pathogenic bacteria worked by the bees into the cerumen walls of their honey pots," contaminating the contents of those pots. He furthermore expressed the opinion that the honey of these two bees, as well as of *Trigona* (*Trigona*) *amalihea* (Olivier) and of *Trigona* (*Trigona*) *fulviventris* variety *guianae* Cockerell, might be "as unwholesome an article of human food as would be honey collected by houseflies, if these scavengers should suddenly become social and take to storing such a substance."

Even poisonous honey, it is claimed, might be therapeutic. Silvestri (1902b, p. 128) has stated that the honey of *Lestrimelitta limão* (F. Smith) which, as above indicated, is usually avoided because of its reputedly toxic qualities, is employed in Matto Grosso, Brazil, as an unguent in cases of rheumatism. According to Ambrosetti (1895, p. 700) the honey of "iratí," which is here interpreted as the equivalent of *Lestrimelitta limão* (F. Smith), produced paralysis. The way to relieve the patient was to give him a dose of the same honey, only heated. Ambrosetti was writing of conditions in the Alto Paraná of Misiones. Furthermore, Cardús (cited by Nordenskiöld, 1929a, p. 170; 1930, p. 198) asserted that the Guaráyí Indians of Bolivia used poisonous honey for the cure of paralysis and in all probability this again has reference to the honey of *limão*.

On the other hand, it was the opinion of H. von Ihering (1903, p. 273) that poisoning by bee honey, instead of relieving paralysis, actually produced an essentially paralyzing effect. In contrast, poisoning by wasp honey resulted, according to that author, in nervous exaltation of a high degree. The effect of poisonous bee honey he described as depressive, that of wasp honey as joyous. But it seems doubtful whether such a line of cleavage can be sustained. Cases of poisoning

from the honey of stingless bees are known, it would seem, only in the case of certain *Trigona*, the honey of *Melipona* not being poisonous. In fact, *Melipona* honey may be of outstanding excellence. Clavigero (1780, p. 107, and subsequent translations listed in the Bibliography) singled out for particular praise the honey known as "estabentùn," gathered from the flower of that name by *Melipona beecheii* Bennett in Yucatan and Chiapas, Mexico. He pronounced it the best of all honey known and indicated that the French of Guarico buy it sometimes for the purpose of sending it as a present to their king.

Peckolt, analyzing the contents of the honey of several species of stingless bees, found that they contained levulose, dextrose, water, ashes, formic acid, dextrin-like substance, and albumin-like substance. Not always were all of these ingredients present, and the proportions varied, but levulose and dextrose usually accounted either singly or in combination for over 50 per cent of the total content. Of the honey of five species that was analyzed, only the unpalatable honey of *Trigona* (*Trigona*) *ruficrus* (Latreille) had as low a combined content of levulose and dextrose as only slightly more than 25 per cent. Among other ingredients in the honey of *ruficrus* (and not listed for the honey of the other species considered) were a mucus of a repulsive taste, constituting about 18 per cent, and small quantities of tartaric acid, a protein substance, and a humus-like insoluble substance. There were present also formic acid and ashes, and water constituted nearly 50 per cent of the total (cited by H. von Ihering, 1903, p. 266).

The amount of honey obtainable from a hive may vary considerably according to the species, size of the colony, time of year, and other possible factors. The average was estimated by H. von Ihering (1903, p. 273) to be from $\frac{1}{2}$ to 2 liters per nest in the case of those that he examined. Hendrichs (1941, p. 371) indicated that in the State of Guerrero, Mexico, the average yield per colony is 1 liter, or in good years 2 liters. Four or 5 pounds per nest is pronounced a fair yield by Hockings (1884, p. 151) for one of the Australian species known as "karbi" (*Trigona carbonaria* F. Smith). But another Australian

species, the "kootchar" (*Trigona cassiae* Cockerell), cited by the same authority (1884, p. 154) may yield in some cases as much as 50 pounds, an astonishing hoard for such a small insect. As much as 10 to 15 liters has been obtained, according to information imparted to H. von Ihering (1903, p. 273), from the nests of certain species, especially what he designated *Melipona nigra* Lepeletier, here interpreted not as *nigra* but as *Melipona schencki* Gribodo, while Bertoni (1911, p. 143) obtained 16 liters from a nest of *Trigona* (*Cephalotrigona*) *capitata* F. Smith. An unusual haul is mentioned by F. Poey (1852, p. 158), namely, no fewer than seven bottles of honey from a well-populated nest of *Melipona beecheii* variety *fulvipes* Guérin. L. Martin (1930, p. 99) reported obtaining 45 kilograms of honey from a nest of a large *Melipona* in the western part of the State of Bahia, Brazil, which is an astonishing yield compared to the 13 to 14 kilograms produced, according to Girard (1879, p. 722), by a populous hive of *Melipona beecheii* Bennett.

In Paraguay, at least, it was customary to store and transport honey of stingless bees in leather sacks. For the purpose a hide was cut in three pieces, tanned, freed of its hairs, sewed together with rawhide cords, and provided at one end with a tube, through which the honey was poured (Hannemann, 1872, pp. 207-208). In Bogotá, Colombia, honey of stingless bees was sold in the market, to which it was brought in bamboo containers (Goudot, 1846, p. 711).

WAX AND ITS USES

The uses of wax were probably limited in pre-Columbian America, but in metallurgy, at least, the Indian discovered without the aid of the white man how serviceable wax could be. Wax was an essential in the goldsmith's art of ancient Mexico. Although wax of stingless bees is not mentioned, there is little doubt that a source so suitable and so accessible would have been used. The text of Father Sahagun, written in the Nahuatl language in the sixteenth century and translated into French by Seler (1892) and then into English by Saville (1920), stated that the ancient goldsmiths "make a mold by means of charcoal and wax, applying to it designs, and in this manner fuse gold and

silver." When the charcoal has been carved into the image of the creature—turtle, bird, fish, crab, lizard—or ornamental collar that is to be represented, "they boil the wax, and they mix it with white copal, by which it becomes very compact. Then they clarify it by filtration, in order that the impurities of the wax, the dirt and the clay which are mixed with it, may be well settled out. When the wax is prepared, they thin it out on a flat stone, and flatten it by means of a cylinder of wood which they roll over it by hand. They thin it out and flatten it on a very smooth stone. When the wax is very thin, like the web of a spider, and is not more thick in any one place, they apply it on the charcoal (which has been carved out) and they cover the charcoal with wax. And they do not do it heedlessly, but they carefully cut a small piece nearly corresponding to the dimensions of the object. They coat over the salient parts and cover the hollows, especially where the charcoal has been carved. The wax is applied (to the charcoal) by means of a bit of wood. And when all is done in this manner, and the wax is put on all parts of the charcoal, they put pulverized charcoal on the surface of the wax. They grind the charcoal powder well, and they spread a rather thick layer on the surface of the wax. And when all is prepared thus, they put on it another covering; the shell which encompasses the mold and encloses it all over. The making of the shell is the last of the processes intended to give the gold its form. This shell is also made of charcoal, mixed with clay, but the charcoal is not finely ground, only roughly crushed. When the mold is enclosed and encompassed by the shell, they let it dry for two more days. Then they put on the spout, which is made of wax also (encompassed by a shell). The latter serves as a drainage canal, by which the melted gold enters. And then they place the crucible on the ground, which is also made of charcoal (and of clay) and which is hollow. In like manner they set out the (mold, with its shell, both made of) charcoal. It is there where the gold is melted, in order then to enter the spout, and being conducted by the latter, to flow below and run out. And when it is melted and run into the mold, and when, for example, they have manufactured a col-

lar, or one of the various objects mentioned in this chapter, they polish it by means of a stone. And when it is polished, they put it in an alum bath. They grind the alum, and they soak in it and wash with it the gold jewel which they have cast. A second time they put it in the fire, and heat it inside. And when it comes out of the fire, they bathe it a second time, and smear it with ointment of gold, which is composed of muddy earth mixed with a little salt, by means of which the gold becomes beautiful and very yellow. And thus they rub and polish and make beautiful the jewel, so that it becomes very brilliant, resplendent, and radiant" (Sahagun, 1920, pp. 125-126, 128-133).

Father Sahagun then went on to relate the status of the art in his day. Fine sand mixed with clay was used as the material for the model. The initial stages in the employment of the wax seem to have been essentially like those described in the previous paragraph. But Sahagun indicated that the jug or scent box which might be the object of the creative efforts of the goldsmith was furnished "with beautiful designs (worked in wax). For the wax lends itself to this better (than clay), and it is more easily worked and modeled into designs." To this end "they make, in the first place, a copy of the relief in wax separately, and when the body of the mold is made, they press (the replica of the relief in wax) on the mold. For the wax is the material with which one can form each detail of design. It may be a wing, it may be the tail of a bird, it may be a flower, it may be a leaf, a handsome ornament of some sort. They press the wax against the surface of the mold and affix it there by means of a small bit of wood called *quauhuitzili* (thorn of wood, point of wood). In about two days all is completed. When all is done in this manner and the wax has been affixed on the entire surface of the mold, they coat it over with pulverized charcoal. After it has become dry, they put the shell on it, made of charcoal coarsely crushed (mixed with clay), and enclose the mold with it. For about two days, they let it dry. Then they put on it the cylinder of wax, called *anilloil* (spout). At first they roll it (to give it a cylindrical form); it serves as a drainage canal by which the gold enters. And when the spout is so placed, they

put the crucible in which the gold will be melted, out on the ground. After everything is done in this manner they put everything in the fire, and they heat it. It is at this point that the wax, which is inside, comes out and is consumed. When the wax has come out and when it has been consumed, they allow the mold to cool again and they place it on a bed of coarse sand. Immediately afterward they turn to the melting (process). They put and place in the pot the charcoal (the mold composed of clay and charcoal). The gold which it is intended to put in, they liquefy separately in a spoon. Thus the work is ended, the task is done. And when the object is made, in order that it be melted and flow out of the crucible, they put it in a bath, prepared with a solution of alum in a copper vessel and they boil it. And if the object is broken in some part, or if it is cracked, they mend separately the damaged sections and they solder on the broken part. Then they scrape it and polish it by means of an instrument of copper. And they immerse it in another alum bath. Finally they polish it and furbish it so that it becomes very brilliant" (Sahagun, 1920, pp. 137-141).

It has seemed worth while to quote nearly in full both the paragraphs relating to the ancient methods of founding and that concerned with the practice in Father Sahagun's day, even though to some extent the latter is repetitious of the former. Nevertheless, new techniques are indicated, and Seler (Sahagun, 1892, p. 417) has pronounced the older technique the more artistic, requiring superior skill; the later one he designates as coarser. In the later process workmanship in wax received greater emphasis than it did in the earlier one.

We turn from the art of creating gold ornaments to the art of "improving" man's countenance. The standards of beauty of certain inhabitants of this earth are often disconcerting to others who have a different standard. Some of the Maya thought that to be cross-eyed enhanced the attractiveness of the individual. Accordingly it was the custom of mothers to attach a small ball of wax to the forelock of a child so that by constant squinting at the pendant object a permanent convergence of the eyes might be achieved (Blom, 1936, p. 123). However, it is open to

question whether in this instance the "wax" was the product of bees. Morley (1946, p. 182) is of the opinion that the pellet was made of resin.

An equally unpleasant custom ascribed to the Maya also involved the use of wax, possibly stingless bee wax. Landa is quoted by Blom (1936, p. 128) as saying: "When the ancient Lords of Cocom died, they cut off the heads, boiled them, took off the flesh and sawed off half of the back of the head, leaving the front part with jaws and teeth; to these half skulls they replaced the missing flesh with a kind of wax, modeling the features to resemble the face of the dead man, and these they kept with the wooden statues where the ashes had been preserved, holding them in great reverence and veneration with their other idols in the prayer rooms of their houses." Again in this instance doubt must be expressed whether the "kind of wax" alluded to can be interpreted as that of stingless bees. Morley, at least, speaks of the substance used as "a kind of resin" (1946, p. 207).

As proof that wax was valued in the civilization of Mexico at the time of the arrival of the Spaniards is the fact that Cortés (1843, p. 113) mentioned it, along with honey, as one of the things offered in the great market at Temixtitlan (Tenochtitlan or Mexico City), where daily more than 60,000 people engaged in buying and selling. To make his meaning unmistakable Cortés used the term "wax from bees," which, considering the time when the report was made in the early part of the sixteenth century, could have meant only stingless bees.

Further evidence of the place of beeswax in the life of the native peoples is the fact that the Aztec Indians had a name for it, "xico-cuitlatl." "Xicotl" is the Aztec word for bee and "cuitlatl" stands for resin. Hence the combination means bee-resin (Sapper, 1935, p. 190). The Maya, too, have a name for beeswax, "cib," which, since the Spanish occupation, has been applied metonymously to candles as well (Roys, 1933, pp. 66, 101, 117).

This transition from the old restricted use of the word "cib" to a new and more embracing employment of the term sheds light on the history of wax and its applications.

Gómara, writing in the middle of the sixteenth century, stated that the native people of Yucatan cultivated large hives and therefore had plenty of honey and wax, but he added that they did not know how to use wax for illumination until they were taught to make candles by the Spaniards (1564, p. 65; 1932, p. 119). Santarén, who is known to have been in the territory of the Acaxee, a mountain tribe of Durango and Sinaloa, Mexico, in 1600, wrote that the Indians "now know how to make of it wax candles for the church," with the implication that probably no use was made of wax by the Indians for illumination prior to their contact with the white men (Beals, 1933, p. 10).

More important still, Bernal Díaz del Castillo, one of the band of adventurers that accompanied Hernando Cortés on his journey of conquest into Mexico, told how the Spaniards erected an altar and how mass was celebrated at the altar by Padre Fray Bartolomé de Olmedo. Díaz went on to say with reference to the attending Indians: "We showed them how to make candles of the native wax and ordered these candles always to be kept burning on the altar, for up to that time they did not know how to use the wax" (Díaz del Castillo, 1908, pp. 190-191). This statement, coming from one who was on the scene at the very start, strengthens significantly the contention that wax candles were introduced by the conquerors.

On the other hand, Redfield and Villa R. (1934, p. 366), or at least the senior author, expressed the opinion that probably "the Middle Americans burned wax as an offering to the gods, as they burned rubber, copal and other substances," although conclusive proof could not be offered; and J. E. Thompson (1930, p. 105) maintained that in all probability wax was used as an offering in pre-Spanish times. Moreover, according to this author some of the odd vessels known as "candeleros" that are typical of the Teotihuacan culture have contained particles of beeswax, possibly indicative of a ceremonial use.

Certain we are of one thing and that is that the use of wax for illumination was greatly stimulated by ecclesiastical demand. The Indians apparently soon learned how useful wax is for the making of candles, and as a

result wax became an important item of commerce not only in Mexico but in other regions, often far distant, as well. One of the chief ways in which the wax of stingless bees was used in South America was for the making of candles (Olivier, 1789, p. 79; Tigny, 1802, p. 76; Latreille, 1818, p. 86; Saint-Hilaire, 1830, p. 371; 1848, p. 164; Lepeletier, 1836, p. 414). Renaud, a physician in Cayenne, French Guiana, recounted how the Indians of that area dipped into molten wax long strips of cotton, left the brew to cool, subsequently rolled the strips, and made candles of them which served for illumination (Olivier, 1789, p. 79; Latreille, 1818, pp. 85-86). Many of the native tribes of South America apparently made candles for sale to Europeans. They were used in rural churches and in the Indian missions (Azara, 1809, pp. 161-162). According to Wied Neuwied (1820-1821, p. 142) the Tapuya Indians of Brazil prepared such candles by winding about a thin core of wax a wick of cotton and then rolling the whole firmly into one mass. The same author stated (1820-1821, p. 219) that the Camacan Indians of Brazil arranged the candles intended for sale in long strings, then placed them in elongated bundles, and finally pasted a coverage of large leaves on the outside. The Patácho Indians of the same country (1820-1821, p. 284) brought great balls of black wax to a settlement for the purpose of making trades.

Saint-Hilaire (1848, pp. 164-165) used candles made of the purified wax of stingless bees and found such candles satisfactory although inclined to drip and give forth much smoke. Landa in the sixteenth century found similarly that the wax of the stingless bees of Yucatan, Mexico, was good "except that it is very smoky" (1941, p. 194). Another who was critical of stingless bee wax was Chagot (1860, p. 358), who estimated that the black wax of *Melipona beecheii* variety *fulvipes* Guérin contained "only 16 parts of the 100 of wax, the rest being resin," and attributed its poor burning quality to this disproportion.

To this day apparently beeswax is used in the Maya village of Chan Kom for making ceremonial candles. According to Redfield and Villa R. (1934, p. 49) the method of making these wax candles is identical with

that used for making those of paraffin. From a wooden ring placed horizontally are hung about 50 wicks and, as this ring is revolved, melted wax is poured over the wicks until the particular diameter desired is attained. Wax candles of this type are either yellow or black, some hives producing wax of darker color than do other hives. Candles of black wax are occasionally lighted at funerals of adults and at that part of the All Souls' Day ceremonies when there is commemoration of the adult dead. Among the Maya of British Honduras black wax candles are considered very sacred and in that region, too, they figure in the All Souls' Day observances. An Indian refused to sell such candles to J. Eric Thompson or exchange them for white ones, explaining that white candles were devoid of a soul (J. E. Thompson, 1930, p. 105). Although in many occupations there was division of labor at Chan Kom, both men and women made candles (Redfield and Villa R., 1934, p. 69).

Candle-making even figures indirectly in the folklore of the Maya Indians. Thus one of the myths gathered by J. E. Thompson (1930, pp. 146-150) at San Antonio, British Honduras, concerns a man who went out wax gathering so that he might make candles for a prospective ceremony. While the man was up in the tree where a bees' nest was located the ape-like mythical animal known as Mahanamatz came along and asked for honey. Both the honey and the wax had been dropped by the man and were on a leaf at the foot of the tree. The man bade the Mahanamatz take the honey but to spare the wax. However, the greedy creature devoured both. To appease the man's anger, the Mahanamatz offered to conduct the man to another tree where an abundance of wax would be found. But when the man had climbed this tree to the level of the hive and had begun chopping to recover the wax, the tree started to grow higher and higher, making it impossible for the man to climb down. Various animals to which the man appealed refused him help. At length the coatís came to his aid and there followed a series of fantastic adventures, in the course of which he escaped to the house of the Chac, whose servant he became. Because he arrogated to himself some of the powers of the Chac, in-

cluding the release of the winds, the Chac dismissed him but, before sending him on his way, gave him a calabash full of honey and a bag of black wax, which would always replenish themselves. The Chac impressed upon the man that, while he might himself revisit the Chac, he must come alone. When the man reached his home, he told a false story to his wife as to where he had been. She was puzzled by his absence and also by the inexhaustible supply of wax and honey. So when he set off again to see the Chac, she followed him. Her presence was discovered by the Chac, who put her through a series of questionings of a very personal nature. As she was about to answer the culminating question, "there came a great wind which swept the woman and her husband off into space." We are not told what happened to the self-perpetuating supply of wax and honey.

Not always seemingly was the wax of stingless bees adapted to candle-making. Thus, an anonymous writer towards the close of the eighteenth century stated (1792, p. 119) that wax of these bees is "always too soft for candles and, therefore, they make use of it instead of corks, to stop up their bottles." He was speaking, it would seem, of a stingless bee on Guadeloupe, possibly *Melipona favosa* variety *variegatipes* Gribodo, which was described a century later from that island. Except for the absence of any reference to corks the passage just cited is curiously reminiscent of a comment made some years earlier by no less a person than Oliver Goldsmith, who in his "History of the earth and animated nature" (1824, p. 146), first published in 1774, had stated that "The wax is so soft that it is only used for medicinal purposes, it being never found hard enough to form into candles, as in Europe."

In commenting on the bees of Guiana, Jardine (1859, p. 292) stated that the natives there convert the wax of the nest of *Trigona* (*Trigona*) *amalihea* (Olivier) into matches. One wishes that his identification of the species could be accepted with confidence, but his accompanying illustration (1859, pl. 27, fig. 1) showing a bright blue bee, more nearly resembling an *Osmia* than a *Trigona*, bears little affinity with *amalihea* as conceived in the present study.

Among the most ancient, persistent, and

ineradicable of superstitions is that based on the making of figurines or pictures of a person against whom some injury is plotted and then of inflicting injury on this image in the belief that more or less corresponding injury will be suffered by the person represented. A thrust of a pin through the abdomen of the image may thus, it is believed, cause pain and discomfort in the stomach region of the intended victim. Burning of the image is likely to bring about the death of the person for whom the image stands. Thousands of years ago this practice was indulged in by the ancient sorcerers of India, Babylon, and Egypt, and later similar nefarious attempts were made in Greece and Rome. This form of witchcraft was known to certain of the North American Indians, such as the Ojibway, for instance, and nearly halfway around the earth cropped up again in a Malay charm, which directed that parings of nails, hair, eyebrows, and other shed parts of the intended victim to the inclusion of his spittle be shaped into his image with wax of a deserted bees' nest (James G. Frazer, 1940, "The golden bough," abridged edition, p. 13). We think of the Elizabethan age—and rightly—as a period when the literary expression of a people reached one of its great culminations. Yet it was also an age of vast superstition that extended even to the uppermost group of society. Queen Elizabeth, for instance, was terrorized by the finding of a wax image of herself which some plotter left in Lincoln's Inn Fields in 1577 and instantly summoned a trusted magician to undo the evil planned (Henry T. Stephenson, 1910, "The Elizabethan people," p. 89). One of the famous Lancashire witches of the Elizabethan age, namely, Old Demdike, confessed that "the speediest way to make a man's life away by witchcraft is to make a picture of clay, like unto the shape of the person whom they mean to kill" and then, after inflicting various torments on that image, destroy it by fire (Henry T. Stephenson, 1910, *op. cit.*, p. 338). Finally one may quote from a play of the period ("The Duchess of Malfi" by Webster) the following lines:

... It wastes me more
Than were't my picture fashioned out of wax,
Stuck with a magical needle, and then buried
In some foul dunghill.

With this type of magic so widespread, it is not wholly surprising to find it cropping up also in the New World. Mention has been made of its occurrence among the Ojibway, who, however, fashion their images of wood. Among the Maya Indians, on the other hand, the figurines are often made of beeswax, and undoubtedly the beeswax came from the nests of stingless bees, for black wax is mentioned. J. E. Thompson (1930, pp. 74-75, 166) gives an illuminating picture of the procedure in the Toledo district of British Honduras. According to his account, the Maya of that region draw a cord smeared with chili and lime about the wax figurine so that it passes over the region of the heart. As the string is pulled tight, the victim is believed to feel the pressure inflicted on his image and to suffer in proportion. The chili and lime are supposed to cause inflammation and so add to the victim's discomfort. The image, it is said, is often introduced surreptitiously into the house of the intended victim.

An interesting variant of this form of vicarious torture is associated also with the Toledo district. Nail parings or hair of the victim are in this case placed in the left hand of the wax figurine. (These vestiges of the victim's person, it will be recalled, also are used in the Malay charm cited above.) In the right hand of the figurine is placed a stone. Five nights of vigil are observed by the sorcerer. On the expiration of this period he goes to the victim's house and places the saturnine statuette above the door lintel. Three more days pass before the figure is capable of fulfilling its evil purpose. In the course of the night of the third day it is supposed to throw the stone it is holding at the victim. This procedure is continued night after night for a month. Whether the victim is aware of the impact of the stone or sleeps on unsuspectingly is not altogether clear. At any rate, the effects of this nocturnal marksmanship become evident, it is said, in the gradual decline of the victim's health, culminating in his death at the end of the fateful month.

Among the Maya of Socotz the story is told of a wicked sorcerer who at one time fashioned nine doll-like figures for the destruction of the people. Seven of these dolls were discovered and rendered innocuous but two es-

caped. Today the people say that the two evil winds bearing sickness to Socotz are caused by these two pernicious figures of wax (Thompson, 1930, pp. 166-167).

Redfield and Villa R. recorded (1934, p. 49) that also at Cham Kom beeswax is used for black magic. Figures are made of it and "There is a belief that children who play with it become somnambulists."

In the highlands of Guatemala the witch doctor shapes an image of wax to represent the individual against whom evil is planned. This image is then placed upside down beside a burning candle similarly inverted (Kelsey and Osborne, 1939, p. 23).

In contrast to these sinister uses of beeswax is one that I commend from personal experience. Years ago when visiting Barro Colorado Island in the Canal Zone, I became familiar with the technique of removing the troublesome ticks that took lodging in one's flesh. The method was to knead a small ball of beeswax and then roll it over the embedded tick, gently extracting the intruder. What was my surprise to learn recently that the same method is employed by the Maya in Yucatan (Steggerda, 1941, p. 148) and very likely in other parts where stingless bees and ticks occur!

It is said that in the Mexican State of Michoacan, and possibly elsewhere in Mexico, carpenters have many uses for wax of Campeche. It is by this designation that the wax produced by *Melipona beecheii* Bennett is known (Storm, 1945, p. 348). This bee (sometimes incorrectly referred to as *Melipona fulvipes* Guérin) likewise produces an excellent honey.

The earliest use by the white man of wax of stingless bees of the neotropics may possibly be attributed to Columbus himself. On his first homeward journey following the discovery, Columbus ran into a storm in the region of the Azores so severe that he despaired of reaching his destination and, drawing forth quill, inkhorn, and parchment, proceeded to set down in brief a narrative of his voyage and its significant accomplishments. This record was then wrapped in a waxed cloth, which in turn was placed in a barrel and cast into the sea, with the hope that it might be picked up if his gallant little ship, the "Niña," failed to outride the storm

(Morison, 1942, p. 422). It is the waxed cloth that possibly links this story with our bees. According to Belknap (1792, p. 118) the wax in question was obtained by Columbus during his sojourn on the island of Hispaniola and "was one of the first finds of his discovery."

Yet one wonders, for Hispaniola (Haiti of today) is not known to have a stingless bee population; or have we overlooked that population, or has it become extinct in the centuries since elapsed? It is remotely possible, of course that by barter the products of the bee reached regions like Hispaniola where the insect itself was not established. Honey and wax were, for instance, among the articles traded by the ancient Maya. Most of the barter by land was, however, with Tabasco and by sea with Ulua (Honduras) and Nicaragua (Tozzer, *in* Landa, 1941, footnote, p. 94).

Peckholt (1893, p. 580) mentioned that in southern Brazil the indigenes used the wax for attaching their feather finery and other things. Later (1894, p. 91) Peckholt indicated that the wax particularly sought for this purpose was the product of "*Melipona longiceps* Smith," which was doubtless a slip of the pen for *Trigona longipes* F. Smith, but may be based on a misconception of the true character of *longipes*, a synonym of *varia* (Lepeletier).

According to Rayment (1935, pp. 512-513) in northern Australia the aborigines decorated their heads by attaching beeswax balls or beads to the ends of wisps of their hair. Similarly they used beeswax to form knobs on tassels of various ornaments, heightening the effect by pressing into the wax the scarlet seeds of a leguminous plant. A further use which certain Australian natives have found for beeswax is as a coping to protect their rock paintings from rain that might otherwise run down the sloping surface of the rock and damage the picture. This is the practice of the Worróra, and in a picture cave of this tribe Love (1930, p. 9) found a semicircle of beeswax over two representations of Wará-ninya, the wedge-tailed eagle.

One of the oddest uses to which beeswax has been applied is recorded, also from Australia, by Wilkins (1928, p. 250). It seems that on the occasion in question it was used as an adjunct of the tonsorial art. An Austral-

ian dandy decided that he would like to have his beard removed, and some of his companions accommodately undertook to carry out his wishes. Beeswax was rubbed on the beard and, while one man sat astride the victim and another held his head on the ground, a third man plucked out the hairs by the roots, glued together in bunches of twos and threes. It is said that the victim steeled himself for the ordeal by keeping up a stuttering chant of "Jesus loves me" half in English, half in his native tongue. One would like to know whether this is a standard method for removing unwanted hair or merely a whimsical exception to other methods.

An Indian tribe (the Pury) living in Minas Gerais, Brazil, used the wax of stingless bees in the fabrication of their arrows and also in making candles for sale to the Portuguese (Wied Neuwied, 1820-1821, p. 142). By the Jicaque Indians of Honduras, I am informed by V. W. von Hagen, the wax of stingless bees is used for blowgun sights and for fixing arrows, and Sapper (1935, pp. 184-185) implied that old wax was used by Indians to stiffen the fastenings of their arrows. A further use for wax mentioned by Sapper was in filling holes (presumably knotholes) in wood. Similar to these uses are those reported of the Ashluslay Indians of the Gran Chaco region of South America, who, according to Nordenskiöld (1910, p. 49; 1912a, p. 49; 1912b, p. 54), employ wax for their arrows, for corks or stoppers, for decorating pottery, and to make all sorts of coatings. Wax was used, on the other hand, by the Chané Indians of the Río Parapiti for making small dolls, which are figured by Nordenskiöld (1910, p. 185, fig. 105; 1912a, p. 173; 1912b, p. 200).

We are apt to think of the serviceableness of anything only in terms of the satisfaction of human needs. It is rather refreshing, therefore, to note that F. Poey (1852, p. 162), after speaking somewhat disparagingly of the wax of stingless bees (or more particularly that of *Melipona beecheii* variety *fulvipes* Guérin) as a medium of illumination, emphasized how palatable it has proved to the Old World pest of beehives, the moth *Galleria mellonella* Linnaeus, which, introduced into Cuba, devours the wax irrespective of its color. In Australia, according to Hockings (1884, p. 155), the moth *Achroia*

grisella Fabricius is very destructive to the combs of stingless bees.

In Cuba wax of the stingless bees, *Melipona beecheii* variety *fulvipes* Guérin, was used in lithography. References to this use of the wax appear both in Felipe Poey's account (1852, p. 169) and also in that of his son, André Poey (1855b, pp. 334-336), and there is further allusion in Burlamaqui (1864a, p. 470). A lithographer of Havana by the name of Marquier was the originator of the plan for using the dark wax of this bee in the manufacture of lithographic ink, and the ink made of this native wax proved more suitable for the purpose than did the imported ink of Europe. Subsequently lithographic pencils were also manufactured from this wax. But these instances do not cover all the known uses for the native wax in Cuba. In addition Felipe Poey noted that it was employed in fastening artificial flowers, in mending shoes, in removing corns, in fastening boys' kites, etc.

Just how corns were removed or "cured" Poey does not indicate, but no doubt the method was the same as that indicated by an anonymous writer of the eighteenth century (1792, p. 119) who pronounced the wax of stingless bees as "very good to soften corns on the feet and warts on the hands." This writer noted that when the wax "has been applied for some time, the corns may be drawn out."

There were other medicinal uses for the wax of stingless bees. The wax of *Trigona* (*Schwarziana*) *quadripunctata* variety *bipartita* (Lepeletier) was, according to Peckolt (1894, p. 90), prized more highly than any other native wax of southern Brazil for salves and plasters, and von Spix and von Martius (1828, p. 523) likewise indicated that the wax of stingless bees is put to these uses. The fragrant wax of "yatei" [*Trigona* (*Tetragona*) *jaty* F. Smith] was used, according to Wapaeus (1867, p. 1157), in Paraguay "only for perfume or in rural medicine."

Writing from Moulmein, Burma, Parish (1866, pp. 198-199) spoke of the preparation and use in Burma of propolis (known as "pwai-nyet"). Boiled in water and softened thereby, it is then given an admixture of petroleum and kneaded until it has the consistency of putty. In this form its principal

use is for caulking boats (Cooke, 1865, p. 252). Parish indicated that "pwai-nyet" in the limited sense is the product gathered by *Trigona* (*Tetragona*) *laeviceps* F. Smith, which is a synonym of *Trigona* (*Tetragona*) *iridipennis* F. Smith. Apparently the use of "pwai-nyet" or "pwe-nyet," as it is sometimes referred to, still persists, for Ghosh in a recent paper (1939, p. 32) stated that Burma has a small inland trade in this substance, which is also known as "bees' dammar." The right to gather the combs is sold each year by the Forest Department and is said to yield an annual revenue approximating 5000 rupees. In addition to its employment for caulking boats in order to make them waterproof, bees' dammar is applied as a varnish. The bee that furnishes this product has the popular name of dammar bee. Ghosh figured the dammar bee and gave as its scientific name *Melipona apicalis*. Although *apicalis* is a *Trigona* (not a *Melipona*), it is a species distinct from the bee (*laeviceps* or *iridipennis*) mentioned by Parish. A South American species, too, furnishes a resinous material prized for the caulking of leaking canoes. This species is *Trigona* (*Trigona*) *fulviventrif* variety *guianae* Cockerell, which, according to L. E. Cheesman, stores large yellow lumps used by Colombian fisherman for this purpose (1929, p. 149). Later (1933, p. 58) Cheesman reiterated the use of wax for caulking in South America but offered no specific examples.

In east Africa, on the other hand, Morstatt (1921, p. 299) found that wax of all species of stingless bees was used to make canes and ropes pliant.

Jacobson noted that in Java the wax of *Trigona* (*Tetragona*) *iridipennis* F. Smith is used by the natives in connection with the process of dyeing known as batik, in which the parts of the fabric that are to be protected from the dyestuff are covered over with wax that, after the dipping, is removed by boiling (Schulz, 1907, p. 67).

It has long been known that ambergris is a product of the sperm whale—an origin sufficiently remarkable but far eclipsed by that assigned to it in a seventeenth century article on stingless bees (Villermont, 1685, p. 1031), in which it is stated: "He (Monsieur Villermont) promises to show me, that

Ambergrise is nothing but the wax, mixt with the Honey, which falls into the Sea, and is beat about in the Waves, between the Tropics." One could almost wish that this fantastic explanation had validity, so that yet another use for the wax of stingless bees might be added to those already cited, for ambergris is (as is well known) a product prized by the perfumer.

In northeastern Brazil (Bahia), along the Rio São Francisco, a very unusual use is made of the nest of a stingless bee known there as "arapuá," a name commonly applied to *Trigona* (*Trigona*) *ruficrus* (Latreille) but used also for certain other members of the subgenus *Trigona*. According to R. von Ihering (1939, p. 75; 1940, p. 403) the compact part of the nest is triturated and cooked. Then this boiled mass is placed in baskets and dipped in the waters that are to be poisoned in order to kill the fish therein. This poison, von Ihering went on to say, is violently toxic to fishes but harmless to mammals and to the majority of lesser creatures. It would be interesting to know what particular element in the nest supplies this quality of deadliness. It is not likely that it is the wax itself as excreted by the bees that harbors the fatal ingredient; more likely it is something that the bees have brought in from the outside to incorporate in the conglomeration of materials that constitutes their nest.

The wax of stingless bees when it issues from the wax producing glands is approximately as pale as that produced by *Apis*, but almost always it is subsequently mixed by the bees with alien materials that give it a darker color. It is true that Bertoni (1911, p. 139) classifies Paraguayan beeswax as follows: (1) of brown color and much mixed with woody materials (*amalihea* and *tataira*); (2) of ferruginous color [various *Melipona* and *Trigona* (*Cephalotrigona*) *capitata* F. Smith]; (3) of clear yellow color and soft (various *Trigona*). In general, however, the wax used in the nest architecture is far from pure and tends to be dark in color. It was the conclusion of F. Müller (1874b, pp. 102-103) that in some species no more than 10 per cent of the building material is wax, resinous substances and clay accounting for the other 90 per cent. It is no surprise that, even in cases where the admixture of foreign materials is

much less, this impure dark wax is often very resistant to blanching. When Azara was making his journey through the South American wilderness in the late eighteenth century, no way was known of bleaching it (Azara, 1809, p. 161). Nor was any blanching method known in northern South America, for Fermin (1769, p. 301) in his account of Surinam shortly after the middle of the eighteenth century indicated that the dark wax of the stingless bees of the region remained permanently dark.

The Count da Barca made repeated attempts, according to Saint-Hilaire (1848, p. 164), to give the indigenous wax of Brazil a light color, yet had not succeeded. On the other hand, Saint-Hilaire observed at Goyaz a workman who had discovered a successful method, which consisted of melting the wax, dividing it into small bits, and exposing these to the sun. He repeated this process 16 times, consuming two to three months in doing so, but in the end the wax was almost as white as that of the domestic honeybee. An effective method of blanching was that, too, which was in force in the province of Chiquitos, Bolivia, as related by D'Orbigny (1839-1843, p. 617): "The wax, at the time when it is brought from the forest, is blackish and soft. To impart the necessary firmness and to bleach it, one subjects it to various preparations. It is allowed to boil a long time with the ashes of plants containing much potash. After this first washing, it is mixed with lime and is thereupon exposed for several months on platforms called tendales. When it has remained the time needed for blanching, it is melted again and shaped into cakes, which are then sent to Santa Cruz. The wax is at that stage white, solid, even brittle. When it is burned, it emits an aromatic odor that is rather pungent and very agreeable. It is reserved up to the present for church uses. In ordinary years—in 1829, for example—the province of Chiquitos had in storage 119,726 pounds of wax."

Not all wax had to be bleached, however. According to Azara (1809, pp. 161-162) a large stingless bee found at Santiago del Estero, in the Chaco, produced a pale wax that could be mingled up to a half with tallow. Inhabitants of the region gathered annually about 14,000 pounds of this wax.

Bertoni (1911, p. 145) spoke of the wax of *Trigona (Plebeia) mosquito* F. Smith as "almost white," and Burlamaqui (1864b, p. 4; cited by Raveret-Wattel, 1875, p. 757) referred to the wax of one Brazilian stingless bee that was paler than that of the Old World honeybee and superior in quality. The bee in question, it was said, nested in hollows of trees in certain regions near the Amazon.

Peckolt made analyses of the ingredients in the wax of Brazilian stingless bees as he did of the ingredients in the honey. The wax of the following species was analyzed: *droryana* and *ruficrus* among *Trigona*, and *fuscata* among *Melipona*. Wax, resin, water, and ashes were present in varying proportions in each case, and usually there was also present a humus-like substance. The wax in each case exceeded 50 per cent of the total, ranging from 52 to 59 per cent. Resin ranged from about 31 to 42.5 per cent of the total. The analyses are based on too limited a study of material to be applied more generally. Some species are known to use other foreign substances than those included by Peckolt, but it is interesting at least to find the wax content so high in the conglomerate material studied. However, the percentages cited did not apply to the brood envelope, where the wax ranged from about 11 per cent to about 20 per cent, and where, in addition to resin and humus-like substances, not to mention plant material, there were in substantial proportions organic substances soluble in water and organic salts (cited by H. von Ihering, 1903, pp. 267-269). In the analyses of the brood envelope Peckolt apparently failed to include an analysis of the brood envelope of *ruficrus*.

The process of preparing the wax in Cuba was described by F. Poey (1852, p. 168). The wax was obtained from the provision containers, which were first thoroughly cleansed of honey and of pollen and, when dry, placed in a pan over a slow fire. The melted part was drawn off, and if any dregs remained at the bottom of the pan, they were thrown away. Another method was to boil the wax in water, and to skim it from the surface of the brew, or to strain it through a linen cloth; but this method, which worked well enough in the case of wax of the European honeybee, is, according to Poey, unsuited in the

case of the dark wax of the stingless bees.

In the Maya village of Chan Kom the inhabitants clarify wax by melting it and then placing it in cold water, whereupon the good wax comes to the surface. "The wax which is no good stays underneath" (Redfield and Villa R., 1934, pp. 49-50). In his account of the Maya communities of southern British Honduras, J. E. Thompson (1930, p. 105) indicated that beeswax, known as "kab," is boiled before being used. There is a superstition that "it should be boiled fasting, but all are agreed that if the boiler should defecate while the wax is being boiled, it will turn bad."

From east Africa used to be shipped from time to time wax that passed under the name of "bumblebee wax"; but as there are no bumblebees south of the Mediterranean region of Africa, the designation was obviously a misnomer. The wax in question (of an inferior quality) was the product of stingless bees (Morstatt, 1921, pp. 283-305).

Although the wax of stingless bees has been adapted to many diversified needs, its field of usefulness is more restricted than that of the honeybee. In a recent article (1944-1945, Trans. Kansas Acad. Sci., vol. 47, p. 193) R. L. Parker mentioned no fewer than 150 regular uses for this product of *Apis* after noting that since the beginning of World War II beeswax had found additional application "in adhesive tape, waterproofing of sails, shells, shell-canvas, machinery going into the tropics, leather boots, and ropes."

DOMESTICATION OF STINGLESS BEES AND RITES CONNECTED WITH BEE CULTURE

Although a number of species of stingless bees have been removed from time to time from their homes in the forest and placed in artificial nests, there is no meliponid species that has been more often adopted by man than the bee that is frequently referred to as *fulvipes*. It was this bee that Huber (1839, pp. 1-26, pls. 1-3) spoke of as "*Melipona domestique*" and that Darwin (1859, p. 225) designated *Melipona domestica*. It is rather a pity that the specific name *domestica* cannot be applied to this bee, for it commemorates its association with man so well, but unfortunately the earliest name (even earlier than *fulvipes*, which is an insular race first re-

corded in 1835) is *beecheii*, described in 1831 by E. T. Bennett.

The popular names applied to *Melipona beecheii* E. T. Bennett are even more numerous than those bestowed upon it by scientists. The Maya Indians probably referred to this bee when they used the term "yilkil-cab," literally honeybee (Tozzer and Allen, 1910, p. 298; Roys, 1931, p. 342). In Yucatan today it is known as "coel-cab," meaning lady bee, and also as "xunan-cab" and "colmena-cab," signifying hive bee (Villa R., 1945, p. 58). Other names that are said to be applied to it are "abeja alazona," "pipioli," and "mimialcuatl" (Sapper, 1935, p. 190). This varied assortment of names indicates how generally recognized are the services of *beecheii* in the communities to whose well-being it contributes. "Cab," which figures in the compound names for bees noted above, may also mean hive or honey, or even earth or land (Roys, 1933, pp. 64, 171), while, according to J. E. Thompson (1930, p. 105), "kab," presumably the same as "cab," signifies beeswax.

An interesting account of the domestication of *Melipona beecheii* in Mexico is given by E. T. Bennett (1831, pp. 358-359) based on the observations made by Captain Beechey. A hollow tree is selected for the purpose and a section of it, 2 or 3 feet in length, is cut off. At about the middle of this hollow log a hole (the future flight hole of the colony) is bored, and the log is then plugged at each end with clay or, according to Oviedo y Valdes (1853, pp. 245-246), with stones intermixed with clay, or, according to Hall (1824 p. 224), with "circular doors, cemented closely to the wood, but capable of being removed at pleasure." The future hive is thereupon suspended horizontally on a tree, and it is not long before a swarm takes possession of it.

Very likely the occupation of a hive through the release of a swarm from a neighboring hive was one of the ways in which domesticated colonies of stingless bees were multiplied. After all, in a wild state it is the only way in which a parental colony can establish daughter colonies. It is the way, too, in which an apiary of the European honeybee adds to the units of its population. However, the occupation of a suitable hollow

by *Melipona beecheii* was usually not left to the discretion of the bee. Huber (1839, p. 22) came into possession of information supplied by bee-keepers of Mexico indicating that there existed yet another and apparently more effective method for propagating the colonies—a method that precluded the possibility that a recalcitrant swarm might refuse to occupy the hollow log intended for its reception. This other method consisted in separating a portion of the brood comb from the parent hive and setting it up "with a handful of old bees" as the nucleus of a daughter colony. Of course, such a new nest would have had to include also a member or members of the royal caste either already emerged or represented among the brood, but apparently the method was successful for it was an established practice in the propagation of colonies not only in Mexico but far down into South America.

According to Bennett, the removal of the honey from one of these artificial hives could be achieved without "the means adopted in Europe for stupefying or even destroying the inhabitants of the hive." The only thing required was to withdraw the plug at each end of the hive and take possession of the adjacent honey pots. One of these artificial hives would yield, according to Bennett, at least two harvests of honey during the summer. However, hives were tapped at other seasons, too. According to Clavijero (1780, pp. 107-108) and Thomas (1882, pp. 115-116) honey was removed from the hives every other month throughout the year. Nevertheless, individual discretion usually dictates more sparing treatment of the bees. A Maya apiarist, master of a native apiary consisting of no fewer than 110 log nests of *Melipona beecheii* E. T. Bennett carefully banked up on a scaffolding of wood under a sloping thatched roof, told me that he gathered the honey only twice a year, in April and in December. This apiary, which I visited in August, 1946, was located between Mérida and Chichen-Itza in the Mexican State of Yucatan (pl. 4, fig. 4). Today, in the Maya village of Chan Kom, honey of stingless bees is gathered in successive months but not throughout the year, the collecting period covering March, April, May, and November (Redfield and Villa R., 1934, p. 49), while among the Popoloca

Indians of Vera Cruz, also, March, April, and May (the dry season) are the favored months.

A Popoluca Indian is required to practice continence for seven nights before opening a hive, seven being the mystic number of this people. At the end of this period, the honey gatherer goes forth before sunrise, smokes the hive with copal, which he burns in a small clay pot, and thereupon removes the honey. After a second smoking, the ends of the hive are sealed, and are kept sealed until the honey gathering of the next year (Foster, 1942, pp. 538-540).

It is astonishing to learn that a similar sexual inhibition is enforced in an African tribe, the Akamba, in Kenya Colony. These negroes, without possibility of contact with the distant Popoluca Indians of the New World, nevertheless impose a like restriction upon the honey gatherer. The requirement for continence applies not only to the owner of the hive but also to any one who assists him in opening the hive to remove the honey. Such a helper is asked to take an oath of abstinence, in force for 10 days beyond the period of honey gathering; 10 days being regarded as the period required before the bees again resume the reprovisioning of their violated home. If at the end of this period the nest has been abandoned or the activities are static, it is proof that the oath has been broken. Then it behooves the bee-keeper to prepare ngondu, a purifying medium, and spread it, together with a piece of mutton, over the beehive. It is stated that ritual abstention like ritual intercourse plays an important role in all Akamba custom, and that accordingly it is in conformity with the general practice of this people to find it extended to beekeeping (Lindblom, 1920, p. 498; Thorp, 1943, pp. 268-269).

The best honey obtainable in Mexico was produced from a flower known as estabentún, previously referred to, which blooms in September. This honey was gathered from hives in the month of November (Clavijero, 1780, p. 107). It is said to be very sweet and liquid and is sold to this day in Mérida, the capital of Yucatan. There is another thicker honey, also much appreciated in Yucatan, which, according to my Maya Indian guide, is derived from a flower known to the Maya as "tah."

According to a report made indirectly to

Huber (1839, p. 22) by bee-keepers of Tempico, a fairly large artificial hive produced annually about 3 gallons of honey. In the environment of Campeche as many as 600 or 700 hives might be assembled, according to von Humboldt (1811, p. 240), in a single apiary. In 1803, he said, there were exported from Campeche to Vera Cruz 582 arrobas of wax.

The extent to which apiculture was maintained in Yucatan in the early years of the nineteenth century may be inferred from the disposition made of property after death. Of the wills drafted by residents of Ebtun in eastern Yucatan some (more particularly those made during 1811 to 1813) have survived in the archives. It is remarkable that in many of these wills the term beehive occurs as one of the principal items bequeathed. Moreover, the term is used not only in the singular but substantially in the plural. More often than not it is in lots of three, six, 10, or a score that the beehives are willed to this individual or that, the multiple heirs often acquiring multiple beehives. Other things associated with the bees, such as wax and the wire masks used by the bee-keepers, also receive mention in the property over which the maker of the will disposes. (Roys, 1939, pp. 57, 295, 329, 337, 341, 343, 347, 349, 351, 355, 365.)

In addition to using hollowed wooden logs, the Mexicans, according to Hall (1824, pp. 224-225), sometimes used cylindrical hives of earthenware, ornamented with raised figures and circular rings. The little flight hole was so molded as to suggest the mouth of a man or of some monster, the head of which was represented in the earthenware of the hive. Above the hole was a little projection that served as a rain shed. Huber, who received a colony of *Melipona beecheii* that had been brought back by Captain Hall, figured such an earthenware hive in his article (1839, pl. 2, fig. 1). The hive is in horizontal position with a supporting cord towards each of its lateral extremities. The head occupies the upper part of the middle region of the hive and rises somewhat above the hive. The mouth, which presumably serves as the flight hole, is at the middle of the cylinder (pl. 4, fig. 2).

Although the art of sculpturing was easier of accomplishment when a soft medium such

as earthenware was available, even the hollow log type of beehive was sometimes ornamented. Thus Oviedo y Valdés (1853, p. 246) described wooden hives of the sixteenth century that on their barkless exterior had sculptured designs and ornamentation in relief, each bearing also the insignia of the proprietor of the apiary.

It is of interest to note that Bequaert (1932, p. 17), traveling alertly in Yucatan, also found hives of the hollow log type which bore ornamentation. In these hives the artificially bored entrance in the center was enclosed by a square surmounted by a small cross carved in wood. Redfield and Villa R., in their interesting record of Chan Kom, a Maya village, also make reference (1934, p. 48) to the presence of a small cross over the entrance hole of the hive and give various explanations offered to account for it, namely, "to show the bees where the door is," "to give good luck to the hive," "to show which is right side up when you move the hive." According to Dame (1941, p. 179), "Crosses also kept evil spirits from mixing with the bees and spoiling the truly delicious honey." His observations were made at Xocempich (place of the pich tree). Among the Maya of east central Quintana Roo, a territory that occupies the eastern section of the peninsula of Yucatan, Villa R. (1945, pp. 57-58) noted similarly that a small cross surmounted the entrance of the hive but in addition he commented on the presence of a wooden cross on top of the apiary itself.

As might well be suspected, the introduction of the cross as part of the ornamentation of the beehive is of ancient rather than recent origin. When in 1530 Alonso de Avila and his small troop of soldiers made their march into southeastern Yucatan, crossing Lake Bacalar, and moving on towards the Bay of Chetumal, they passed through areas rich in honey. In order to punish the Indians for their resistance and also by way of registering disapproval of the rebellion of Gonzalo Guerrero, a Spaniard who, captured by the Indians, had "gone native" and linked his fortunes with those of his captors, De Avila seized the beehives of the region and redistributed them among his men. But here is the interesting thing: he directed his followers to mark the hives with a cross so that these hives might

be recognized as the property of Christians (Blom, 1936, p. 72). Thus in this instance the cross seems to have been used to place the stamp of legality upon a wanton seizure of personal property.

One is inclined to think that sometimes, notwithstanding the instance just cited, the use of a miniature cross as part of the insignia on a beehive may have been an act of exorcism rather than an assertion of proprietorship. In Hall's time, at least, the earthenware hives were ornamented with what Hall (1824, pp. 224-225) described as "monsters," and it seems not unreasonable to suppose that these earthenware hives followed, in respect to their ornamentation, the standards of an earlier tradition. Does it not appear plausible that these "monsters" may have represented a diety or deities connected with apiculture? If so, a spiritual purging would occur when the heathen symbols were discarded and in their place was substituted the true cross. In much the same manner the site of a demolished heathen temple became sanctified ground when on it was erected a mission church or cathedral.

The influences of the Christian religion on apiculture may also be traced in such a custom as that of gathering the honey on Good Friday, which is the practice of the Kekchi Indians of Alta Verapaz, Guatemala. They remove the honey from the nest of a small black *Trigona* that they have domesticated, called "kerk-cam," and seemingly Good Friday is the only day in the year when the bees are forced to part with their store (Sapper, 1935, p. 186). H. Friese identified "kerk-cam" as *Trigona mexicana* variety *alisfumatis* (Sapper, 1935, p. 187).

In this connection it may be recalled that Good Friday is considered a lucky day in which to remove honey bees in Devonshire, while in Cornwall it is the contention that their removal on any day other than Good Friday will be fatal to them. In the Vosges Mountains, Good Friday is the day on which people clear up the area where the beehives are stationed. It is the custom at the same time to place on each hive a small cross made of wax or a branch of box that has been blessed on Palm Sunday. This procedure is supposed to guarantee the prosperity of the hives and to prevent their inmates from

straying at the time when they swarm (Ransome, 1937, pp. 229, 239).

The individual hives of the domesticated *Melipona beecheii* Bennett, to the number sometimes of several score (Redfield and Villa R., 1934, p. 48), in other cases around 50 (Bequaert, 1932, p. 17), in one instance said to number "over 400" (Norman, 1894, p. 511), while even this number is eclipsed by the 600 to 700 already cited from von Humboldt, are assembled in rows on racks built of poles. Two such racks are placed at an incline in order that they may give mutual support, and in this position they suggest an A-frame (Roys, 1943, p. 42). Then to shield the hives from sun and rain, there is built over the racks a palm-thatched shelter consisting largely of roof with no walls. These apiaries usually are at some distance from the dwelling of the owner, set up in a corner of the house lot, but they are not placed in maize fields or outside of the village. In nearly every instance they extend east and west. Although the explanation given is that this orientation protects the hives more effectually in the event of rain, Redfield and Villa R. suggested that originally perhaps the orientation had a religious significance.

Tozzer and Allen (1910, p. 300) likewise referred to "a specially constructed shelter" for the hives. An illustration of a shed built by the Mixtec Indians of southern Mexico for the accommodation of their hives is published by Starr (1899, pl. 58). According to that author (1900, p. 140), "The beehives are cylindrical foundations made of sticks tied together, which are then wrapped in matting and hung to the sides of houses or arranged upon supports over which protecting thatches are constructed."

In other cases the section of tree hollow containing a wild swarm is transferred from the forest and suspended beneath the eaves of the house in which the lucky finder lives, or it may be hung in any other shady spot, even under the roof of a hog or chicken shelter. This is the practice among the Popoluca Indians of Vera Cruz, Mexico, but before the wild hive is taken from the forest it is customary to sprinkle water on the cut ends, an act which, according to the belief of these Indians, assures good production of honey on the part of the bees (Foster, 1942, p. 538).

Almost certainly it is *Melipona beecheii* Bennett to which the Popoluca Indians refer as "abeja real," or royal bee. In the department of Magdalena, Colombia, on the other hand, the name "abeja real" is reserved for *Melipona interrupta* variety *salti* Schwarz, perhaps because its honey is of such excellent quality. *Melipona interrupta* is closely related to *Melipona beecheii*, and both apparently are proper recipients of the flattering designation that has been given them (Salt, 1929, p. 434).

In the State of Guerrero, Mexico (one of the regions from which the Aztec king collected his tribute of honey), the cultivation of the native bees continues today, although on a more restricted scale than of old. There, according to Hendrichs (1941, pp. 367-368), apiculture is practiced in the region that lies along the right bank of the Río Balsas. Two species of bees are favored, one of which may be recognized from the description as probably *Melipona beecheii*. The hives are transported from the forest and hung on the outer wall of the houses. Honey is removed generally in April and, if the year be a good one, a second time in October.

According to Hendrichs, furthermore, bee culture after the ancient manner is still pursued by the Indians along the borderline of the Mexican states of Jalisco, Colima, and Michoacan, while Vera Cruz and Tabasco, not to mention other neighboring states, are also centers of apiculture after the pattern of the long ago (Sapper, 1935, p. 191). Yucatan, in early days the area preëminently associated with bee culture, still holds an important place in honey production, but the Maya of the Toledo district of British Honduras have discontinued the domestication of bees (J. E. Thompson, 1930, p. 105).

Melipona beecheii E. T. Bennett is the bee commonly installed in artificial hives in Yucatan. It is not, however, the only stingless bee that man has domesticated. To some extent *Trigona* (*Scaptotrigona*) *pectoralis* Dalla Torre is also present but always in isolated hives, well removed from the large apiaries of the other species (Bequaert, 1932, p. 17). Other stingless bees that, it is said, are cultivated by the natives of Yucatan include a *Partamona* and *Trigona* (*Tetragona*) *jaty* F. Smith (Stempell, 1908, pp. 736-737).

Five honey producing Hymenoptera in

addition to *Melipona beecheii* E. T. Bennett are mentioned by Redfield and Villa R. (1934, pp. 49-50) as being favored by the Maya villagers of Chan Kom. Of these, four ("xik," "ehol," "yaxich," and "niitcab") are presumably stingless bees. The first three are sometimes placed in hives and hung under the palm-leaf eaves of houses, but they are not placed on the racks with *Melipona beecheii*. It is always hazardous to attempt to identify a species from brief accompanying characterizations but the reference (p. 50) to "xik" as small and black, and "their wings—just a little bit of their wings—white" leads me to believe that "xik" is *Trigona* (*Tetragona*) *nigra* variety *nigra* Cresson. "Niitcab," said to smell like limes and to produce honey that is unpalatable, conjures up *Lestrimelitta limão* (F. Smith), although one is puzzled by the reference to its building a nest of mud in the branches of trees. Perhaps "niitcab" should be interpreted rather as *Trigona* (*Nannotrigona*) *testaceicornis* variety *perilampoides* Cresson, for *testaceicornis* is said to have "a pleasantly aromatic lemon-like odor" (Ducke, 1925, p. 403). The reader is referred to the discussion of *Lestrimelitta limão* (F. Smith) for further comment. Other native bee names supplied by Villa R. (1945, p. 58) are "kantzac," "bool," "munl," the hives of which are located in the earth. Another name for "ehol" is "xibi-cab," and the Maya believe that anyone who swallows one of these bees alive will thereby acquire the power of locating wild colonies more readily.

In the district of Temascaltepec, located in the southwestern corner of Mexico, Usinger (1935, p. 667) observed yet another bee that had been domesticated, namely, *Melipona fasciata* variety *guerreroënsis* Schwarz. True, only a single hive was noted, but there would seem to be good reasons for extending the culture in this instance, for Usinger referred to the disposition of the bees as "being as sweet as the product of their labors, the so-called 'miel virgen.'" However, virgin honey has been ascribed also to bees other than *guerreroënsis*.

Not only in Mexico, but also in nearby areas of Central America, *Melipona beecheii* is preferred as a honey producer by the native inhabitants over other stingless bees. In Honduras, for instance, on the authority of

V. W. von Hagen, this bee has been domesticated by the Jicaque Indians (pl. 4, fig. 3) more extensively than any other stingless bee, although *Trigona* (*Trigona*) *fulviventris* Guérin is also favored (von Hagen, 1943, p. 44). The Aztec Indians of El Salvador, according to the observations of C. V. Hartman (1901, p. 297), have domesticated two species of stingless bees, housed in small gourd shells suspended from the walls of their huts. Bee-keeping has been known in British Honduras, according to Gahne (1902, p. 947), "as far back as the history of the colony," and Gahne went on to state that the bees "were kept in the logs in which they first built, the honey being drawn at intervals by probing into the log with a sharpened stick." This is the very same technique of extraction described by Diego de Landa, Bishop of Merida from 1573 to 1579, showing how retentive of ancient methods has been the native bee culture of the New World (Landa, 1941, p. 193).

Although this extension of apiculture into the neighboring countries is in evidence today, it would seem that in earlier periods some of these regions were dependent for honey largely on exports from Yucatan. Both Honduras and Tabasco received their supplies from this area. According to Roys (1943, pp. 53-54) in his account of colonial Yucatan, there was a considerable amount of wild honey gathered in the forests of Honduras, but there was no domestication at that time of the stingless bee. Little or no honey was produced in Tabasco according to the published records of the sixteenth century and, when candles were required, the Spanish colonist had to procure the wax from Yucatan. By 1676, however, Dampier recorded both domestic as well as wild bees in Tabasco, and the fact that the former were housed in hollow sections of tree trunks is pretty strong evidence that they were stingless bees and not introduced honeybees. The extremities of the hive were closed with a detachable board, but the most interesting variant from the standard adopted in Yucatan and elsewhere was the upright orientation of the nest, in accord with the natural habit of the bees, instead of the customary horizontal placement of the hollow log (Roys, 1943, p. 105).

In the sacred hut of the Lacandon Indians of Chiapas, Mexico, a people belonging to the

Maya-Quiché linguistic stock, are hollow log hives from which honey used in making a ceremonial drink, "balché," is obtained. The honey produced in this hut is never used for secular purposes, such use being regarded as sacrilegious. Hollow logs are media for the reception of the ingredients of "balché," with substitution of sugar-cane juice as an ingredient when honey is not obtainable. The log containing the mixture is left uncovered, and fermentation is allowed to proceed, sometimes for no more than one day. Sticks are then laid parallel across the log, and on these in turn are placed palm leaves. Rain must be prevented from reaching the contents of the log. While the fermentation is going on, a chant is delivered before the open log. (Tozzer, 1907, pp. 115, 124-125.)

In the Maya village of Chan Kom, when they prepare "balché," four pieces of bark of the balché tree (*Lonchocarpus longistylus* Pittier), about a foot in length, are pounded by means of sticks and then put in a jar with two "jícaras" of water and a cup of honey. The mixture is permitted to stand for three days and is then sampled. If it is not of the right quality, more honey is added, and it is then left for a further period until it acquires a yellow color (Redfield and Villa R., 1934, p. 38).

In the village of San Antonio, British Honduras, "balché" is known also as "baluch." When the bark of the *Lonchocarpus* tree, which in Spanish is designated "pitarilla," is not available, there is substituted for it the bark of the pine. According to J. E. Thompson (1930, p. 104), strips of the green bark are washed and then left to dry for an indefinite time, the longer the better, and even months may pass before the bark is put to use. It is then beaten with a hammer or other suitable instrument so that the sap may be released. Equal amounts of honey and of water are then added, and the mixture is permitted to ferment for from four to six days. One would judge from the longer period of fermentation allowed in San Antonio that the resulting brew may be rather more "heady" than in the communities of Mexico. Landa (1941, p. 92), on the other hand, seemed to have been under the impression that it was the tree that imparted potency to the drink, making it "strong and stinking."

He specifically referred to the root of the tree, but it is the bark that is used.

It may be mentioned in passing that the name "balché" was applied not only to the ceremonial drink but is also the name of a site in Yucatan where stands a ruined stone pyramid (Roys, 1939, pp. 24, 121, 125), while according to Antonio Mediz Bolio one or more country homes in Yucatan also bear this designation, which is derived from "bal" (meaning concealed) and "che," which is the word for tree (Hofl, 1930, p. x).

Ceremonial rites connected with beekeeping were anciently practiced by the people of Yucatan. For the celebration that took place in the month of Tzec the preparations were made in the month of Sotz or Zotz or Tzoz (considerable latitude of choice is permitted in the spelling). The priest and those who assisted him in the ceremony were obliged to fast during this period of preparation; for other celebrants fasting was optional. On the day of the festival those participating gathered in the house where the ceremonies were to be enacted. They had as mediators Hobnil and other Bacabs, deities that were stationed, one at each of the four points of the earth, to uphold the sky. Four plates with pellets of incense in the middle of each and painted all about with certain figures representing honey were among the offerings. The purpose of the ceremony was to bring abundance. Wine was served in quantity, a wine, incidentally, in which honey was an important ingredient (Landa, 1864, pp. 292, 297; 1941, pp. 156-157; Thomas, 1882, pp. 116-117; Tozzer and Allen, 1910, p. 300; Joyce, 1914, p. 267; Nordenskiöld, 1929a, p. 175; 1930, pp. 203-204; Gates, 1937, p. 73; Tozzer, 1941, pp. 156-157).

It may be said in passing that Hobnil, just referred to, was the special patron of those engaged in apiculture (Blom and La Farge, 1926, p. 132) and that the name Hobnil means primarily something hollow, being a term applied in Yucatan for the beehive, probably because beehives are made of hollow logs (Roys, 1933, p. 171). The name Bacab, on the other hand, has been assigned various origins, but Tozzer (1941, p. 135) pointed out that patronymics, in so far as they can be traced, run strongly to floral and faunal origins, including a number of insect designations, and

drew the conclusion that "cab" in the combination Bacab means "bee" rather than "earth," as has been contended. Among the Maya the god of the bees is called Kananholkan, signifying keeper of the door of the sky (Tozzer, 1907, p. 124).

The ceremony above described held in the month of Tzec was not the only one dedicated to apiculture. In the month of Mol yet another festival was celebrated, similar to that previously held, only in this instance the appeal to the gods was to provide flowers for the bees (Landa, 1864, p. 306; 1941, p. 159; Tozzer and Allen, 1910, pp. 300-301; Gates, 1937, p. 76). The ceremony may have been one inspired by concern and gratitude—concern lest the bees should be deprived of an essential of their life, and gratitude for the beneficent part bees have in supplying man with a toothsome and nourishing product. But one inclines to think also that these people of the long ago were perhaps aware that nectar gathering and honey production were not unconnected, and that in appealing to the gods for abundance of flowers for their bees, they were also indirectly petitioning for a rich harvest of honey for themselves.

Ceremonies connected with bee culture have persisted. Although cattle, deer, and other wild animals used as food by the Maya each have their supernatural protectors, it is only the deities devoted to the domesticated bees that are the objects of important religious observances. Some or all of these deities are believed by some people to be balams and the apiaries are their property. Hence it behooves man by prayer and offering to atone to these deities for having taken honey, which by right is theirs, and for having touched the bees, which belong to them, in the act of removing this honey. Redfield and Villa R. (1934, pp. 116-117) attribute the restraint of the natives of Chan Kom in taking only a limited amount of honey from a hive to this recognition of the proprietary rights of the bee gods, but it may be said in passing that such restraint also works to the advantage of those exercising it by leaving sufficient food to assure the perpetuation of the bee colony instead of destroying what is the insect equivalent of the goose that laid the golden egg. At Tusik in Yucatan offerings are made on the opening of a beehive, but unaccom-

panied by full rituals (Redfield, 1941, p. 97).

Of the ceremonies performed on behalf of the bee deities and of the nature of these deities Redfield and Villa R. (1934, p. 117) give this report:

"As with the harvest, so with the honey of the hives; for each year's yield which man secures, he owes a ceremonial offering to the gods. One of the ceremonies made for the gods of the bees (u hanli cab) fulfills this obligation. The other (u hedz luumil cab) is made when the hives are moved, or when a new hive is established. If these ceremonies are not performed, the patrons of the apiaries are likely to visit the owner with sickness; then the owner will make the ceremony in atonement, so as to get well. The custom is to move the hives only on Saturday, the belief being that only on Saturdays do all the bees return at one time to the hives, to rest as men do. Indeed, the claim is made that it is by observing the bees that one may tell that it is Saturday.

"The gods of the bees take the form of large bees and dwell in the east (the chun caan) as do the rain-gods. Their number and their names are not matters of general common understanding and agreement. Some laymen speak only of the 'balam-cab,' of the 'noh-yum-cab' ('great lord bee'). One h-men gave the following account: The noh-yum-cab is the principal ruler; under him are all the other bees of the world. Then come a class of bees known as x-mulzen-cab. These dwell in a certain place at Cobá, where there is much red earth and many nests of bees (such as the wild bees make). This place is inaccessible and protected by a tiger-like animal with a long tongue, called hak-madz, who devours anyone who attempts to enter the place. It is the business of the x-mulzen-cabob to inform the noh-yum-cab of everything that happens in the apiary. [How ardently a student of the Meliponidae would welcome the cooperation of the x-mulzen-cabob!] Then come the bees known as bolon-hobon ('nine (?) hives'). Their task is to cure the bees who have been injured when honey is taken from the hives. If on a Saturday a bee is reported missing, one of these bolon-hobon goes out to search for the lost one, to cure or revive him. The next class is known as balam-cabob. They remain at the beehives and keep away

the evil winds. When u hedz luumil cab is made, it is to make offerings to the noh-yum-cab so that he will direct the balam-cabob to move to the new site and there continue their protection of the apiary."

The following myth gathered by J. E. Thompson (1930, pp. 156-157) during his sojourn among the Maya of British Honduras is very closely linked with the functions ascribed to the "bolon-hobon" as outlined in the previous paragraph. A man who went out to search for bees in the company of his faithless friend was deprived of his eyes by that friend's treachery. Wandering through the forest he became aware of the angry hum of bees and realized he was near a colony that had recently been robbed of its honey. Sitting down on a fallen tree trunk, he waited. After night had set in, there appeared on the scene the Lord of the Bees, who made the following promise to the mutilated occupants of the ravaged nest: "I will cure all those who have broken wings or legs, who have been crushed or who have lost their eyes." The Lord of the Bees was as good as his word. All the wounded bees that came to him were made whole once more. Then the blinded man begged that he, too, might be permitted to see again and the Lord of the Bees restored his sight. The folk tale then goes on to tell how the wicked friend came to a violent end but, as the bees had no part in his destruction, we leave the story truncated at this point.

A footnote that Redfield and Villa R. supply to the name "x-mulzen-cab" is to the effect that a layman interprets this name as that of the place of red earth at Cobá, where the bee gods dwell. The "balam-cabob" this layman calls "balam-kanche," and adds the name of still another god of the bees, namely, "kuna."

Cobá, which has been alluded to more than once in this narrative, no doubt played an important role in the ceremonial life of pre-Columbian Yucatan, and J. E. Thompson (1932, p. 4) emphasized among the rituals of particular interest that have persisted from ancient times and are still practiced in parts of northwest Yucatan the propitiation of certain Cobá deities in the beekeeping ceremony.

Roys (1943, p. 75) bore testimony to the fact that the modern Maya still invoke the

bee gods known as "mulzen-cab" or "mulzen-cabob" (Roys, 1933, p. 64) whom they regard as supernatural bees. These divinities are said to dwell in the ruins of Cobá and thus are presumably the same as the "x-mulzen-cab" previously referred to. Another spelling is "muğencab" or "mucencab." Roys stated that he had identified the insect-like god of Cobá and others in eastern Yucatan as these "muzencab."

The ceremony referred to above as "u hanli cab" ("dinner of the bees") takes place at intervals of four years, although the bee-keeper apparently sometimes puts off the ceremony until reminded by illness that his tardiness has angered the bee gods. As recorded by Redfield and Villa R. (1934, p. 145; Villa R., 1934, pp. 253, 289), on the evening preceding the performance of the rites, the "h-men" (an individual who discharges the functions of priest and of shaman) invites the lords of the bees to attend on the following day. On the altar, erected beside the hives, he thereupon places a "homa" of "zaca," the "homa" being a gourd vessel and "zaca" a preparation of maize customarily offered to gods and spirits (the "zaca" in this instance has been sweetened with honey). An invocation is then delivered. The men present wait for an hour or two so as to give the gods the opportunity of taking the gracia or spiritual essence of the zaca. During this interval the "h-men" drinks the rum that has been furnished by the giver of the ceremony, and thereafter the "zaca" is distributed among all those present.

On the following morning those taking part bring corn meal to be made into the ritual breadstuffs, and one or more fowls are provided as an offering by the giver of the ceremony. Either 13 or in some instances nine homa of "balché," the old ceremonial beverage, are put on the altar by the "h-men," who offers it to the gods with the words:

As he kneels, the priest-idzac delivers it, he passes the cup around, here to the table of Noh-yum-cab, there at the four corners of the sky at the right hand of God the Father. Amen.

The breads are taken from the earth oven, and soup known as "kol" is made ready. The foods to be offered are subsequently arranged on the altar.

Two "idzacs" are appointed by the "h-

men," and one of these is usually the giver of the ceremony. Taking his place between the two "idzacs," the "h-men" offers the food to the gods as he recites a prayer calling upon each of the classes of bee divinities. At the conclusion of the ceremony the "h-men" and the "idzacs" move nine times around the hives, carrying the ritualistic food. "Balché" and some of the "kol" are sprinkled over the hives while the "h-men" repeats the prayer. The fowl or fowls (sometimes hens, sometimes turkeys) offered on these occasions are themselves forced to partake of the "balché" as part of the act of consecration. An interval may elapse between the cooking of the ritualistic foods and the resumption of the ceremony, which as a result extends over many hours.

Not always do things run smoothly. In Appendix A to "Chan Kom—a Maya village" by Redfield and Villa R. (1934, p. 289), Villa R. tells of a "h-men" who, when called upon to deliver the customary prayer, was so incoherent owing to the anise he had been imbibing that the prayer dissolved into disconnected phrases and finally trailed off into a monologue on socialism and political office-holders. Each of the "idzacs" in this instance moved in opposite directions, one clockwise, the other counterclockwise, as they executed their nine revolutions about the altar. At intervals the "idzac" struck the hives with a branch of "zipche" plant, while the "h-men," notwithstanding his inebriated condition, kept track of the number of circlings by means of leaves of "yinche."

The ceremony known as "u hedz luumil cab" is one of the lesser observances and hence does not necessitate the making of an earth oven, which is used especially in festal cookery. Instead, one of the other culinary techniques is applied, namely, the griddle or "comal," on which the ritualistic breads are prepared. These breads are of two kinds: large tortillas known as "cham-cham-uah" that have ground squash seed over one of their surfaces and are folded over once, and large thick tortillas called "pim-pim-uah" that consist of dough mixed with squash seed. Hens are offered and for each such fowl there is a heap of 13 "cham-cham-uah" and one gourd containing "zaca." Three "pim-pim-uah" are combined with the broth to form the "kol."

As in the ceremony "u hanli cab," previously described, an altar is erected beside the beehives. To each of the four corner posts a "jícara" of "zaca" that has been sweetened with honey is attached, and a fifth "jícara" is hung before and above the altar. Then "zaca" is offered, followed by an offering of "balché," the hen is consecrated, foods are set down on the altar and dedicated to the gods, and finally these foods are consumed by those who have taken part in the ceremony.

The following invocation is used by a "h-men" in offering bread stuffs and other foods to the gods of the bees in the "u hanli cab" ceremony (Redfield and Villa R., 1934, p. 356). Incidentally this invocation, in line 2, seems to confirm the interpretation that "x-mulzen-cab" is a place, not a divinity:

Be thrice greeted when falls the word to Noh-yum-cab,

Be thrice greeted when falls the word at X-mulzen-cab,

Be thrice greeted when falls the word to the Balams, at his ruined temple—at his fallen (bee-seat), his bench, to Nine-Hives, to him who greedily sucks. Thrice be greeted when falls the work to the great Chaac, to the great Balam, at the four corners of Heaven, there at Coba. When the word falls (to) the great Chaac, great Balam, at the great audience-chamber at Chichen.

Because bees were under the protection of certain deities, they were treated with thoughtful consideration so that the anger of these deities might not be aroused. In removing honey in the Maya village of Chan Kom in Yucatan care was taken not to injure or kill any of the insects. If one of them became honey soaked, solicitude was shown by drying it and then freeing it. A bee drowned in honey was buried in a wrapping of leaf (Redfield and Villa R., 1934, pp. 50, 117).

War among the bees might even portend evil for their owner. In the village of Piste, which is located close to the Maya ruins of Chichen-Itza, a native woman was seen weeping when her husband's bees began to fight and kill one another. Her concern was not so much for them; she wept because she thought their pugnacity betokened the early death of her husband (Steggerda, 1941, p. 59).

Various hieroglyphs in the ancient Mayan Codex Tro-Cortesianus (Troano) have been

interpreted by Brasseur de Bourbourg (1869, p. 120), Thomas (1882, p. 116-117), Stempell (1908, pp. 735-737), Tozzer and Allen (1910, p. 301, pl. 2), Ransome (1937, pp. 260-271), and several other investigators as representing stingless bees and their products.

Brinton ([1895?], pp. 59-61), in commenting on the bee pictures of the Codex Tro-Cortesianus, offered this interpretation:

"In view of the prominent part which the Venus-year plays in the calculations of the Codices, it has surprised students that no pictorial figures of this bright star appear on their pages. On this point I have some suggestions to make.

"In one part of the Codex Troano (pp. 1-10) there are a great many—nearly fifty—pictures of an insect resembling a bee in descending flight. These pages have been explained by Thomas as relating to apiculture and the festivals of bee-keepers, and by Seler, who rejects that rendering, as referring generally to the descent of deities to receive offerings. Direction downward is indicated not only by the position of the insect, but by the accompanying hieroglyph, which reads *caban*, the first syllable of which, *cab*, means 'downward.' My suggestion is that in this bee-like insect we have an ikonomatic allusion to the Evening Star, which, as I have already stated, was sometimes called *xux ek*, 'the bee or wasp star.' "

In support of this viewpoint, Brinton went on to say that the object towards which the insect descends is either a fire or a figure suggestive of the conventional representation for clouds. Thus he drew the conclusion that the Evening Star is represented in these associations as descending "to join the departed orb of day."

Bunge (1936, pp. 305-322) also linked the bees of the Codex Tro-Cortesianus with the period ruled by the planet Venus, and listed 13 bees, one for each of the 13 months of 20 days that made up the period of Venus, lasting 260 days.

"The book of Chilam Balam of Chumayel" (a sacred text of the Maya of Yucatan that was named after their last and greatest prophet, Balam, who lived during the last decades of the fifteenth century and probably into the sixteenth century) contains many references to bees, beeswax, and honey as

they figure in Maya mythology (Roys, 1933).

In the "Popol Vuh," the sacred book of the Quiché, one of the Maya tribes, it is related (Joyce, 1914, p. 243; J. E. Thompson, 1927, p. 44) that the only occupations permitted the conquered people of Xibalba by the heroes Hunabopu (or Hunahpu) and Xbalanque were the making of pots and the keeping of bees, which as Ransome pointed out (1937, p. 263), is probably proof of the importance attached to apiculture.

Another pertinent story from the "Popol Vuh" has been vividly retold by Ransome (1937, p. 263): "The Quiche relate that the ancestors of their tribe, whose town lay on a mountain, were once besieged by a neighboring tribe, so they entrenched themselves as well as possible. Then they made wooden figures which looked like men, placed them on the ramparts, hung shields and bows on them, and put gold and silver crowns on their heads. Then they hunted for hornets, wasps, and bees, and brought them to the camp. They put the little creatures into four great calabashes and placed these round the town; they were to help in defeating the enemy. Now the enemy sent spies to the town, who reported that they had seen a few men—the wooden figures—but not many; so they came in great numbers to attack the town and had nearly got in, when suddenly the covers of the calabashes were taken off and the insects flew out like smoke, flew in the eyes, noses and mouths of the enemy, hung on their legs and arms, which they stung and so obliged the men to throw down their weapons, when they were attacked and killed by the men of the town."

In spite of the reference to stinging, which may have been the contribution of the hornets and the wasps that were included in the aggregate, no doubt there were among the bees species that belonged to the Meliponidae. The fact that the insect assailants entered the eyes and ears of the enemy confirms this conclusion. The tale is of particular interest because it indicates that in the New World as in the Old man may have used bees as an ally in combating an enemy or in defending a besieged town. Several such instances dating from classic times to the inclusion of World War I have been reported, but the insect whose combative fury contributed to the

victory was in each such case the honeybee. On the other hand, in the instance from the "Popol Vuh," if hive bees were used, they must almost certainly have been stingless bees.

Nests of honey producing Hymenoptera are sometimes borne about in processions in the State of Michoacan, Mexico. For instance, the wild-honey collectors of the Tarascan village of Cherán bring home the nests they have gathered during the day and, in preparation for the fiesta that is in prospect, they fashion two structures known as "katáarakua." These consist of two poles crossed at one end to form a V. Thereupon cross pieces are made fast to the poles, and this framework is used to support the honeycombs, "held in place with a large net similar to the fish nets of Lake Pátzcuaro." At the top of each of these V-shaped structures are placed the two largest honeycombs, to be borne about the plaza in ceremonial fashion. Also cigarets, handkerchiefs, and other coveted objects are placed at the top of a well-greased pole to be the prize of him who first succeeds in making the slippery ascent. These objects are known as the "panal," or honeycomb (Beals, 1946, p. 126).

According to Storm (1945, pp. 341-342), it is occasionally the custom for a girl to carry "a great gray bees'-nest" in the fiesta of La Magdalena celebrated about July 22, also in the Mexican State of Michoacan. One suspects a survival of some ancient religious observance, but the reference to "gray" suggests the likelihood that the nest was that of a honey producing wasp, not improbably *Nectarina lecheguana* (Latreille).

Among the Popoluca Indians of Vera Cruz, Mexico, it is the surmise of Foster (1942, p. 539) that there may have been at one time a god of bees, although today his memory has been forgotten, and Christ and San Isidro alone are regarded as patrons of the stingless bees. Certain superstitions, however, persist. In December the bees are believed to weep because the end of the year is approaching, and to pacify them it is necessary to burn copal. The "abeja real" (probably *Melipona beecheii* E. T. Bennett) is particularly prone to take offense, and if certain rules and rituals are not observed will desert her hive and fly to the forest. Domestic squabbles, it is claimed, are repugnant to this royal bee, and

a man who has two or more wives is, therefore, rarely successful as a bee-keeper. This is reminiscent of the Central European superstition that bees will not thrive if the family of their owner is quarrelsome or if one member deceives another (Ransome, 1937, p. 170).

Foster is also authority for the statement that when "elotes" (maize roasting ears) are ripe in the "milpa," it is customary among the Popoluca for a man to cut seven ears, make seven tamales and consume them with the aid of his wife before more "elotes" are eaten as part of the daily diet. But those who have hives of the "abeja real" mix honey with the grains of maize, which have been previously cooked, and eat this combination instead of tamales. Anciently, it is believed, this custom may have been more prevalent than it is today.

As further evidencing supernatural associations, the opinion is held by the Popoluca Indians that ability to discover bee trees varies with the individual and that aptitude in finding nests is to some extent an indication of divine favor (Foster, 1942, p. 539). On the other hand, the Ashluslay Indians of the Gran Chaco region in South America, before setting forth on a search for wild beehives, were wont to pierce with a sharp stick the region above the eyes until the blood flowed, in the belief that through this incision their chance of finding the desired prize was improved (Nordenskiöld, 1910, p. 49; 1912a, p. 49; 1912b, p. 54). In this tribe, as in so many others, it is the men who gather the honey and the wax.

As the many references throughout the paragraphs preceding make clear, Yucatan was a thriving center of apiculture from pre-Columbian times, persisting, little changed, to the present. Although it seems not unreasonable to conclude that domestication of stingless bees had its origin among the Maya, Sapper (1935, p. 192) does not exclude the possibility that the first beginnings may have been among the Mixtec or their neighbors. The production of honey extended southward beyond Mexico, and J. E. Thompson alluded (1930, p. 105) to the domestication of the bee even in Panama in the pre-Spanish period. Among the Cuna Indians of Panama the word for bee is "acha" and honey is "achanisa" (Nordenskiöld, 1938, p. 658).

Not only the native population but the Spaniards, too, on their arrival appreciated the products of the bee. Diego de Landa stated that during his stewardship as bishop towards the end of the sixteenth century each Indian was required during that period to deliver a supply of wax as tribute to the Spaniards, and that such tribute was gathered in the forest from nests in hollow trees and the clefts of rocks, as the bees in domestication did not produce a sufficient quantity (cited by Stempell, 1908, p. 736, and by Ransome, 1937, p. 261).

In imposing tribute of wax on the indigenes the Spaniards were in a way only carrying on the tradition of the Aztecs, who required tribute of honey from the native communities they had overcome. In the *Codex Mendoza* are listed the quantities which had to be delivered to Montezuma by the communities living in the "tierra caliente" far below the lofty seat of power of the Aztec king. These communities in a region located today almost entirely within the State of Guerrero were called upon to deliver annually 2400 jars of honey (Hendrichs, 1941, p. 367). Tribute of honey was also paid by the towns of his province to the "halach uinic," the "real man" or ruler of one of the independent states of the Maya (Roys, 1933, p. 190; 1943, p. 61), but the payments were not onerous.

In 1783, to protect the natives from exploitation, a government edict was issued forbidding what were known as "repartimientos" of cloth and wax, thus abolishing the practice of advancing money for the delivery at some later date of goods in quantities onerous for the producer. It is interesting to find that this method of committing the Indian to an oppressive obligation included specifically the delivery of such a product as beeswax (Roys, 1939, p. 58).

In Chan Kom in Yucatan there is division of labor between men and women. It falls to the lot of the men to do all agricultural work, to take care of the cattle, and to hunt. Bees are entrusted to the care of men, who construct the hives, establish new colonies, and remove the honey. The women, however, are charged with the boiling of the honey (Redfield and Villa R., 1934, pp. 68-69).

Although Mexico and Central America

evidence the most consistent attempts in the New World to domesticate stingless bees, in South America, too, apiculture was practiced. Although many a wild nest was pillaged so ruthlessly that no opportunity was given the nest occupants to recuperate, there are other cases where the insect producers of honey were treated more considerately and wisely. When the Caingua or Caigua Indians of the Alto Paraná, Misiones, find, according to Ambrosetti (1895, p. 700), a bees' nest in the forest, they do not utterly destroy it but leave enough of it to induce the bees to persist in their efforts at replacement, so that when they again visit the spot, they may exact another enforced contribution. Such an act of foresight, as Nordenskiöld pointed out (1929a, p. 172; 1930, p. 201), may be regarded as the initial step in the domestication of bees.

Other tribes, however, went further and, as did the Mexicans, actually domesticated stingless bees. Nordenskiöld (1929b, p. 285) mentioned that the Makino Indians of Brazil bear from the forest entire nests in order to suspend them near their huts, while other tribes, such as the Paressi of Matto Grosso, the Menimehé of the Rio Japurá, Amazonas, and the Mixtec of Central America, construct veritable hives for raising the bees. These practices, Nordenskiöld went on to state, were derived, it would seem, not from the white population but are traceable to a pre-Conquest apiculture. The cradle of this apiculture in the Americas appears, according to Nordenskiöld, to have been Central America, from which it spread subsequently to South America, while Foster (1942, p. 542) regards it as "certainly within the bounds of reason to suggest that domestication or near-domestication of the wild bee may have occurred independently in two or more places."

Transportation of a hive from the forest and its installation in an Indian community represented an important step towards apiculture, and the actual construction of hives for the accommodation of colonies a still more advanced stage in the progress of beekeeping. However, solicitude for the welfare of the bees occasionally manifested itself in an even more interesting way. It is said that the Chorti Indians of Guatemala, after bearing a wild hive from the forest, actually plant nearby a

number of flowering plants. As a rule, wild shrubs, but in other instances fruit trees, are provided so that the bees may have easy access to them and produce more honey (Wisdom, 1940, pp. 68-69). The orchardist in our own communities is frequently advised to set up a colony of bees so that his apple trees may be adequately pollinated and thrive, but equally significant seems to me this instance of a lowly people which plants flowers and trees primarily for the benefit of the bees, although the flower as well as the insect is bound to prosper as a result of this thoughtful act. Wisdom referred to the most important species of the wild bees as the "talnete," and, according to his description, these bees are "small and black, have no sting, and are native to eastern Guatemala." The description might apply to several *Trigona*, but one thing is certain, the "talnete" is a fortunate bee, enjoying the cooperation of so understanding a bee master.

Certainly, domestication of stingless bees had taken place in Venezuela before the Europeans arrived on the scene. Oviedo y Valdés (1852, p. 331) cited Bishop Rodrigo de Bastidas to the effect that in Venezuela the Indians kept bees in hives made from large calabashes as early as 1540. Just as the hollow log type of hive persisted from ancient times to modern in Mexico, so the calabash (the fruit of *Crescentia cujete*) has had an enduring tenure in South America. Nordenskiöld (1929a, pp. 172-173; 1930, p. 210) called attention to the fact that Roquette-Pinto (1919, pp. 13, 341, fig. 3) depicted such a hive that was still in use among the Paressi Indians of the State of Matto Grosso, Brazil. However, its use was not confined to South America; the Aztec of El Salvador also had the calabash, and Sapper (1935, p. 188) indicated that its territorial range included Central America. In addition to the calabash, beehives made of other materials likewise appear among the South American records.

Beehives of clay, it is said, were noted by a soldier of the sixteenth century in the Valle de Caldera, near the Sierra Nevada de Santa Marta, Colombia (Nordenskiöld, 1930, p. 202; Sapper, 1935, p. 189). The number of clay beehives counted by this individual, it is stated, reached the incredible total of 80,000. Seemingly apiculture, in so far as it involves

stingless bees, was at a higher peak in the New World at the time of arrival of the white man than it is today.

In addition to the calabash and the vessel of clay, the hollow log type of hive was also employed in northern South America. Nordenskiöld (1929a, p. 174; 1930, p. 202) and Sapper (1935, p. 189) pointed out that Whiffen had noted among the Menimehé on the Rio Japurá hives made of hollow tree trunks that these Indians prepare for swarms to occupy. The hives are kept inside the moloka or tribal hut of the Menimehé so that bee products may always be available (Whiffen, 1915, p. 51).

More than 100 years ago the inhabitants of Sabará in Minas Gerais, Brazil, had hit upon a scheme, "which has succeeded perfectly," for multiplying the colonies of stingless bees, namely, that of removing from a hive some of the combs and establishing these in a new hive "which one takes the precaution of perfuming with incense" (Saint-Hilaire, 1830, p. 372). Years later H. von Ihering (1912, p. 2) commended this method of expediting the formation of colonies (which recalls one of the methods employed in Mexico, see p. 144) by stating that his pupil Marianno had successfully achieved the artificial parturition of populations containing new brood combs and that this method seemed to him the only feasible one for increasing the populations of desired stingless bees.

Yet in the interval between Saint-Hilaire and H. Von Ihering others, too, had found this method of propagating hives a satisfactory one. Nearly half a century after Saint-Hilaire it is mentioned by Raveret-Wattel (1875, pp. 750-751) as one of two successful ways of bringing about the multiplication of hives. Raveret-Wattel's account is based on a communication of Salzedo, who was stationed in Colombia. According to Salzedo, it is a part of the upper combs of the partitioned nest that is transferred to the daughter hive. The physogastric queen is not transferred but is left in the parental hive. Some provision jars are also installed in the daughter hive, which is then suspended at the very spot formerly occupied by the parental hive. The large number of workers absent at the time the parturition was made enter the new hive upon their return from their foraging and thus an

adult population is acquired in addition to the transferred brood.

In the alternative method mentioned by Raveret-Wattel, the combs were apparently left intact in the parental nest. However, provision jars were removed in part and placed in the prospective daughter hive with the defending adult bees that had attached themselves to these jars, and the precaution was taken carefully to transfer to the daughter nest also the physogastric queen, so that new brood might be reared in this new nest. The nest thus prepared was then hung, as in the case of the first method, on the site of the parental nest, so that the new nest might increase its population by gathering in the returning foragers. Both nests apparently thrive ultimately. The parental nest, placed at some distance from the daughter nest, requires a few weeks for its recuperation. At the end of such a period a new surgical operation can be performed. Demonstrating the success of the method is the fact that Salzedo obtained eight successive hives in this way from a single original wild stock. Nevertheless, the method outlined in the previous paragraph, providing for the removal of brood as well as provision containers to the daughter hive, but with the exclusion of the gravid queen, was the method more usually employed by Salzedo and always with satisfactory results.

It is interesting to find that the precaution mentioned by Saint-Hilaire to the effect that the new hive should be perfumed with incense was also deemed indispensable in Bahia. According to Brunet, this was done in order to discourage a particularly destructive parasite from gaining admission to the hive (cited by Raveret-Wattel, 1875, p. 751). Judging from the adoption of this custom in widely separated areas and its persistence over the years, the custom may well have had a wide geographic range and also a considerable span in time.

Somewhat comparable is a custom practiced in British East Africa. To induce a swarm (in this case no doubt a swarm of *Apis* rather than of stingless bees) to occupy a new hive, the prospective home of the colony is fumigated by burning an aromatic wood, the odor of which is pleasing, or at least is thought to be pleasing, to the bees (Lindblom 1920, p. 495). The steps taken by the African

natives of the Wadschagga tribe to induce bees to enter the cylinders provided for their reception are recorded by Gutmann (1909, p. 206). As a lure ripe bananas are placed in the tubular entrance to the hive so that the wood may become impregnated with the pleasing odor. Some *Trigona* bees are partial to bananas, and it seems not improbable that honeybees, of which Gutmann was speaking, are at least not averse to the aroma. Certainly this method of attracting them would seem at least as effective as the chants that are addressed to the insects in the hope that the plea therein voiced may be heeded by the honey makers.

The honey of *Trigona* (*Tetragona*) *jaty* F. Smith takes high rank among the products of stingless bees, and it comes as no surprise, therefore, that this species has been domesticated. Nimuendajú-Unkel (1914, p. 340) recorded seeing a wild nest of this species that had been brought from the forest to a settlement by Apapocúva-Guariní Indians of southern Brazil. According to Bertoni (1911, pp. 139, 143), who between 1890 and 1894 successfully domesticated many species of *Trigona* at Yaguarasapá, Paraguay, *jaty* was the species that is domesticated most easily. Both Nimuendajú-Unkel and Bertoni may, however, be referring not to typical *jaty* but to *Trigona jaty* variety *fiebrigi* Schwarz. Dr. A. Alfaro was good enough to send me a photograph of a nest of typical *jaty* that he had established in a box at his homestead in Costa Rica.

A bee favored for domestication in northern Brazil is *Melipona fasciata* variety *scutellaris* Latreille. According to Brunet, a landowner in the interior of the State of Rio Grande do Norte had hollowed out the larger papaya trees in his plantation and in them had established nests of this bee (cited by Raveret-Wattel, 1875, p. 737). Nine different species of stingless bees were maintained in a semi-domestic condition by Brunet himself in Bahia. To facilitate the removal of the honey, Brunet cautioned, a hole should always be made near that part of the nest containing the honey jars and then plugged until access to the area is needed (cited by Raveret-Wattel, 1875, p. 749). Thus in Bahia, as in Mexico, the endeavor was to assure the continued existence of the hive, with periodic

requisitions of honey, instead of destroying the producer in order to obtain once and for all the accumulated hoard.

It was *scutelleris* that Marianno singled out for particular praise as a honey producer of preëminent quality in a little article (1910a, pp. 14-18) in which he published specifications for an artificial hive especially adapted for the domestication of stingless bees, with supplementary directions as to how to go about the task of transferring a colony in the wild state to the man-made structure intended for its reception. While *scutellaris* was favored by some Brazilians, others were partial to another *Melipona*, namely, *interrupta*, which was domesticated by those living along the Amazon (Le Cointe, 1922, p. 383).

According to Nieuhoff (1813, p. 732), a hollow pipe was used by the Brazilians, among whom he sojourned towards the middle of the seventeenth century, for the removal of the combs (doubtless he means the honey) of a bee known as "eiruku" that built its nest in the cavities of trees.

In addition to domesticating the stingless bees, periodic exploitations of accessible hives in the forest sometimes take place. According to Goudot (1846, pp. 710-711), in New Granada (Colombia) parties of honey gatherers twice a year (April and May, and October and November) scoured the woods for honey and wax. Honey thus acquired often found its way to the market in Bogotá. The same author (1846, p. 713) informs us, however, that an undescribed *Trigona* of the subgenus *Tetragona* had been domesticated in New Granada (Colombia), so that apiculture was maintained in spite of these periodic plunderings of bees in the wild state. Indeed it is not unlikely that a favored nest was spared on one of these excursions of destruction and thus gave rise to domestication.

While visiting the missions in the central part of the province of Chiquitos, Bolivia, D'Orbigny (1839-1843, pp. 614-615) was able to observe the systematic manner in which the Indians explored the primeval forest for bees' nests. Organized bands from each mission would set forth each year from June to September, carefully combing a given area for honey and wax. So successful were these forages that only rarely did such a band, which consisted of 10 to 20 natives, fail to

bring home sufficient wax to enable each of the participants to deliver the 75 pounds that the state exacted from him. The Chiquitos Indians, in addition to plundering the stingless bee nests and destroying them, would often carry off a whole colony and domesticate it. It is stated by D'Orbigny (1839-1843, pp. 615-616) that in several houses in Santa Cruz, Bolivia, he saw such colonies housed in vases.

In Brazil, too, the inhabitants periodically scoured the forests for wild honey. Gardner (1846, p. 327) commented on his arrival at a little Brazilian settlement named Morrinhos in the State of Goyaz: "This was the season in which the people go to the woods in search of honey; it is so generally used that after leaving Duro, a portion was presented to us at almost every house where we stopped."

The craving of the natives of Misiones, Argentina, for the wild honey of stingless bees is described somewhat perfervidly by Spegazzini (1909, pp. 62-65), who himself collected 14 distinct species of honey producers in that province: "The greatest diversion and keenest pleasure enjoyed by the rural peon is that of honey gathering. For a spoonful of honey he is ready to work an entire day around a trunk and often endangers his life. One cannot estimate the risk which people are prepared to take in the mountains for the sake of honey. All that is needed is that a peon observe a small portal of wax or a cleft in a trunk to make him go immediately for a hatchet and to overturn or at the least destroy a beautiful trunk of the most valued species."

In Mexico and Central America, too, organized groups engage in honey gathering. In the Río Balsas region of Guerrero, Mexico, as many as 10 men known as "mieleros," or honey gatherers, band together in the dry season and, equipped with burros laden down with food supplies, empty bottles, axes, and other equipment, scour the uninhabited mountain country for weeks, chopping down bee trees they have been lucky enough to locate and filling their bottles from the honey flowing out of the wrecked nests (Hendrichs, 1941, pp. 366-367).

In Cherán, a Tarascan village in the Mexican State of Michoacan, gathering of wild honey is the one collecting technique still

considered important. During certain seasons of the year, especially in the late spring and fall, specialists in honey gathering known as "panaleros" spend many weeks in this task. Beals (1946, pp. 13-14), who recounts their activities, speaks of the skill of these men in locating nests by the flight of the bees, but allusions to stinging, to pendent nests, to the absence of wax in the nests, and to combs rather than honey pots, incline one to the belief that the "bees" may have been wasps, possibly *Nectarina lecheguana*. Nevertheless, the climbing technique should be recorded, for it would be equally helpful whether the nest was that of a wasp or of a stingless bee: "Once a comb is located, the *panalero* usually climbs the tree and knocks the comb down. If the tree is large he cuts notches in the trunk with a small special-type ax, tying himself with a riata or a length of rope while he chops. The rope is not tied, but passes around the tree trunk and the two ends are held in the hands. The *panalero* holds the rope tightly while he edges up the tree. Then, with a skillful motion, he throws the loop of rope higher up the tree trunk. Once the comb is reached, the *panalero* covers his face and hand with a blanket and taps the comb until the bees leave. The procedures are regarded as highly dangerous. *Panaleros* are always careful to take a good rest before climbing a tree. They are also particularly attentive to their saint, San Anselmo, who is believed to protect them. The danger of the occupation is increased by the fact that the *panalero* always works alone and in case of accident could expect no rescue."

Among the Chorti of Guatemala honey gathering enjoys the status almost of a fixed occupation, a number of families being engaged in supplying the market at Jocotan with wild honey (Wisdom, 1940, p. 69).

Certain tribes recognized property rights in wild honey. Thus De Wavrin (1926, p. 20) in recounting the ways of the primitive Indians of the basin of the Paraguay stated that, when a man located a wild swarm that had not yet reached the peak of honey production, he marked the site, and this indication of his claim was sufficient to restrain others from gathering the honey. In due time, accompanied by his wife, he would chop down the tree and collect his property. According to

Wappaeus (1867, p. 1157), three species of stingless bees were "kept as tame bees" in Paraguay. To safeguard his discovery of wild honey a Popoluca Indian of Vera Cruz, Mexico, blazed a tree on the opposite side of the trail (Foster, 1942, pp. 539-540).

Many tribes were very dependent upon wild honey of stingless bees. The almost monotonous frequency with which honey is mentioned by Tessman (1930) as constituting a food in the case of tribe after tribe among the Indians of northeastern Peru indicates what an important article of diet it is to this very day. Nordenskiöld, whose painstaking contribution to the history and geographical distribution of beekeeping by the American Indians is particularly recommended for perusal, was of the opinion (1929a, p. 171; 1930, p. 199) that those tribes, such as the Guayaqui Indians of Paraguay, that possess stone axes, notwithstanding the fact that they neither cultivate the ground nor make dugout canoes, find these implements primarily of use in cutting into tree trunks where bees' nests are obtainable. He furthermore cited the case of the Tsirakua Indians of the northern Chaco, who, from odds and ends of pilfered metal, including such inappropriate things as wagon-wheel cotter pins, improvise crude chisels by means of which they chip out a hole sufficiently large to gain access to bees' nests in the trunks of trees. In addition to the stone ax the Guayaqui Indians above mentioned employ a yet more ingenious device for extracting the honey from the recesses of the nest. It is a long-handled brush (Nordenskiöld compares it to a shaving brush) that is thrust into the nest and then brought to the surface impregnated with honey. Such eating brushes, only shorter, Nordenskiöld saw in common use among the Ashluslay Indians, likewise of the Gran Chaco (1910, p. 54; 1912a, p. 53; 1912b, p. 59). One wonders whether, after all, Father Gumilla's seemingly preposterous story of the monkey who plunged his tail into the nests of stingless bees in order to soak it in honey really could have had some basis in fact (see p. 99).

The Guayaqui and Ashluslay Indians are, however, not the only aboriginal people that have devised brushes for extracting stingless bee honey. The Victoria River tribes of Australia tie a bundle of vegetable fiber or

pounded bark to the end of a long stick and force this into the nest. When the honey pots are reached, the stick is turned around and around so that the bushy end becomes thoroughly soaked with honey. Thereupon the stick is withdrawn, the honey adhering to the fiber is squeezed into a receptacle, and the process of inserting the stick into the nest is repeated (Basedow, 1925, p. 146). A brush improvised by pounding the end of a stick was used for lapping up wild honey by the Australian natives that accompanied Sir Hubert Wilkins (1928, pp. 246-247).

A legend told by an Indian on the Río Beni in Bolivia is recorded by Nordenskiöld (1929a, p. 171; 1930, p. 199). It is to the effect that an Indian woman forced her arm into the nest of a stingless bee located in a tree hollow but was unable to withdraw it and thus she perished and remained suspended from the tree by her arm. Nordenskiöld believed that the legend might have been based on a real happening. In any event the episode points to the interest evinced in honey gathering.

Undoubtedly the introduction of the honeybee (*Apis*) into areas of South and Central America has tended to discourage the domestication of stingless bees. Fifty years ago Peckolt (1893, p. 580) indicated that in Brazil, where formerly certain species of Meliponidae were maintained, the inducement to do so no longer existed and that indeed, where the honeybee had been introduced, available wild hives tended to disappear owing to the slaughter of the unarmed stingless bees by the formidable aliens. Peckolt was writing from southern Brazil, where the European honeybee is particularly abundant, but it is likely that his remarks apply more forcibly today and to a much wider expanse of territory. However, as we had occasion to note in a previous section (pp. 87-88), the honeybee is not always the victor in these combats.

In the Old World, too, domestication of stingless bees has been tried by the indigenes. Thus in the Kilimanjaro region of Africa, according to Morstatt (1921, pp. 286, 295), "bee-cylinders" are placed in the trees to attract *Trigona erythra* variety *togoënsis* Stadelmann, the honey of which is greatly desired.

Such is the relish of the Australian aborigines for the products of the stingless bees

that, according to Tillyard (1926, p. 305), they will follow one of these bees for miles in the hope of locating the nest. In order to make the bee conspicuous and hence an easier object to pursue, the Australian native has devised an ingenious technique, recorded by Major Mitchell: "They would catch one of the bees and attach to it, with some resin or gum, the light down of the swan or owl; thus laden, the bee would make for the branch of some lofty tree, and so betray its home of sweets to its keen-eyed pursuers, whose bee-chase presented indeed a laughable scene" (cited by Jardine, 1859, p. 284). Instead of attaching a feather, a wisp of cotton might serve similarly to make the flight of the bee conspicuous (Rothschild, 1878, p. 121). It is even recorded that on occasion spider silk is employed (Barrett, 1941, p. 109).

DISTANT VOYAGES AND ATTEMPTS TO ACCLIMATIZE STINGLESS BEES

Again and again in perusing the literature of the stingless bees one comes upon records of their successful crossing of the Atlantic or of their achievement of the long journey from the Malayan regions through the Indian Ocean, the Red Sea, and the Mediterranean to some European port. How did these involuntary travelers, whose arboreal home was suddenly destined for shipment to some remote lumber yard for cabinet-making or other uses, manage to survive the length and the perils of such a voyage? The vast stretches of ocean are flowerless, and insects whose lives are ordinarily dedicated to the gathering of pollen and nectar would suddenly find themselves deprived of all opportunity for these activities. To be remembered, too, is the fact that the majority of the records that have come down to us belong to an era before the age of oil and electricity and the advances of marine engineering had made possible the production of the ocean "greyhounds." Many of these records belong to the time when the sailing ship was still the usual means of travel. Months might be consumed in a voyage from some distant tropical port to one of the maritime cities of Europe. In fact, it is in larger units than months that those who came into possession of the nests calculated the passage of the time required to round out the journey, which might in-

volve the slow passage along river systems of the interior of Central or of South America before reaching the port of shipment and further delays there before a vessel with suitable capacity arrived to take over the cargo.

Thus Bigg, who as early as 1834 exhibited live specimens of "a very pretty and apparently undescribed" species of *Trigona* before the October gathering of the Zoological Society of London, was of the opinion that a year and a half might have elapsed since the bees left their native Brazil (Bigg, 1834, p. 118). Tomaschek (1879, pp. 582-587; 1880, pp. 60-65), who was the recipient of a colony of stingless bees, figured that the entire time consumed from the felling of the tree containing the hive to its delivery in Germany might have exceeded a year. Upon reaching a European port there was the further trip to destinations in the interior. Cornelius (1875, pp. 184-185) calculated that the trip from Rotterdam, the port of reception, up the Rhine to Düsseldorf and Elberfeld, where the shipment of logs, including the one with his bee colony, was finally delivered, might have alone consumed six to eight weeks.

One asks again, How did the bees fare during such long periods when replenishment of their food supply was impossible? In rare instances honey was made available to them by a fellow voyager of the human species desirous of delivering them in good condition to some interested prospective recipient in Europe (H. Müller, 1875b, p. 52). In a great many cases, however, the fellow voyagers of the bees were unaware even of their existence, and discovery came only belatedly when the colonies reached Europe. During the long journey the bees must have been dependent on their stored provisions, and in these cases the industry of the bees in the period prior to their maritime adventure proved ultimately a great boon to them. But ocean voyages are the great exception as far as the bee world is concerned, and one may wonder a little at the diligence of the bees in piling up supplies in their tropical homeland where high temperatures tend to prevail and there is nothing compared to the barrenness of our own northern winter. It might seem that, where plants are available for honey gathering throughout the year, the need for provision against the proverbial rainy day

would be superfluous. But the rainy day (or rather the rainy season) in many tropical regions is very literally rainy and must to some extent be as deterrent to the outdoor activities of insects that are dependent on the sunshine as is the cold of the temperate and more polar zones.

Rau, it is true, noted (1933, p. 27) bees of *Trigona* subgenus *Partamona* in full activity gathering honey during a heavy rainstorm, but such activity is probably exceptional. Green (1905, p. 1316) said of the Cuban stingless bee: "It flies in bad weather when the *mellifera* does not venture out." In contrast Drory (1874, pp. 281-286) observed in the case of his transplanted colonies that in days that were windy or rainy the bees remained at home. Peckolt (1894, p. 88) reported that a colony of *Trigona* (*Plebeia*) *mosquito* F. Smith, which ordinarily opened its nocturnally sealed entrance to the outside world each morning when the weather was fine between 5:30 A.M. and 6 A.M., deferred doing so on rainy days, and on one day of exceptionally heavy rain kept the entrance closed throughout. The same observer indicated the only occasional emergence on rainy days of individuals of what he doubtfully designated *Trigona* (*Tetragona*) *jaty* F. Smith. According to Michener (1946, p. 190) the only species in Old Panama that "remained active during a light rain" was *Trigona* (*Trigona*) *fulviventrís* Guérin.

Flowers, too, have their seasonal fluctuations of abundance so that even in lands of relatively continuous plenty the stingless bees would seem to derive advantage from the accumulated stores of provisions (Goudot, 1846, pp. 712-713; Gronen, 1881b, p. 332; Marshall, 1898, p. 132). Moreover, in some regions, especially towards the southern extremity of their range, the months are not uniformly warm. According to Holmberg (1887, pp. 256-257), the stingless bees of Misiones, Argentina, remain within the hive during the "cold months of May, June, and July and only exceptionally do some audacious individuals venture forth into the cold atmosphere." On the other hand, Schrottkey (1901, p. 209) affirmed that in the São Paulo region of Brazil even on the coldest June days *Melipona* and *Trigona* might be noted as they pursued their floral trail.

That in spite of industry and favoring conditions shortages of provisions may sometimes occur is evidenced by a nest of *Trigona* (*Plebeia*) *molesta* (Puls) which was examined by H. von Ihering. This author stated (1903, p. 224) that the nest in question, received by him on October 5, 1900, was almost completely devoid of pollen and wholly devoid of honey. Von Ihering added that apparently the provisions had been used up in full during the over-wintering period.

To return to our bee immigrants, we have noted that the arrival of a stingless bee colony with living occupants was announced by Bigg as early as 1834, but as a matter of fact this is not the earliest recorded importation of nests of these bees. Two hives of *Melipona beecheyi* Bennett were previously brought from Mexico by Captain Beechey (E. T. Bennett, 1831, pp. 358-359). They were described as "completely formed and occupied."

An early instance of the introduction of stingless bees into France is related by Blanchard (1849a, pp. 86-87). According to that writer, a lady who evinced an enthusiasm for natural history had the patience and devotion to bring with her from Rio de Janeiro to Paris two hives of stingless bees, identified as *Trigona* (*Trigona*) *pallida* (Latreille) and *Melipona quadrifasciata* variety *anthidioides* Lepeletier. Supplied with honey on the long journey, they were installed on arrival in Paris in the Rue Saint Lazare, where they soon set to work in a neighboring flower garden gathering their provisions. The *Trigona* species soon succumbed but the *Melipona* persisted from the month of May until the close of September. One is perhaps justified in inferring that this interesting attempt at acclimatization occurred not long before it was reported in 1849. It is very possibly the first attempt to make the stingless bees acquainted with the French metropolis.

The period when colonies of stingless bees arrived with greatest frequency or at any rate when they were most provocative of discussion was during the fifties, sixties, and seventies of the last century. As early as 1854 the Société Zoologique d'Acclimatation, in the very first year of its existence, gave consideration to a proposal communicated by Sacc to the effect that there be introduced

into France hives of two Brazilian species of stingless bees abundant in Pernambuco and in Bahia (Sacc, 1854, p. 180). In the following year there came further persuasive counsel of this character. André Poey, of the famous family of Cuban naturalists and a member of the society, emphasized the practical advantages to be derived from the establishment of New World meliponids in southern France as well as in Algeria (1855a, p. 295). However, it was not in the more clement environment of southern France but in the metropolis itself that these introduced visitors from the New World were seemingly first exhibited. In 1855 the Parisian populace had been given a foretaste of the interest offered by stingless bees through the exhibit of the wax and honey of an Australian species shown at the World's Fair of that year (Raveret-Wattel, 1872b, p. 428). It was not long before live exhibits followed. A colony of what was designated, very possibly incorrectly, as *Melipona fasciata* variety *scutellaris* Latreille from Rio de Janeiro, Brazil, was installed by Lucas (1862, pp. xxxvii-xxxviii) in the greenhouse of the museum at Paris and subsequently, when the bees were attacked by ants, in the laboratory of entomology. At the time of his report the hive was two months old, having been received late in August, and was rapidly declining. A number of the New World stingless bees that F. Smith described (1863a, pp. 497-512) originally "were exhibited, together with samples of their honey and wax, in the Brazilian court of the International Exhibition of 1862." It is not clear whether these exhibits were of living hives or of dead specimens. In 1863 a living colony of stingless bees (*Melipona fasciata* variety *scutellaris* Latreille) was brought to Paris and established at the Musée d'Histoire Naturelle, but the insects perished at the first cold (Drory, 1872b, p. 157; Figuier, 1867, pp. 434-435). Hamet (1864b, p. 302) and Blanchard (1868, p. 464) likewise referred to the establishment of not merely one but two colonies of stingless bees brought from Brazil in the Jardin des Plantes, which adjoins the museum. In this case, too, the bees perished with the first cold spell. Also in Paris were maintained in the summer of 1874 *Melipona fasciata* variety *scutellaris* Latreille and *Trigona* (*Scaptotrigona*) *postica* Latreille (Girard,

1876a, p. 194; Raveret-Wattel, 1875, p. 740). Both of these colonies were presumably those which Drory (1874, p. 282) stated he had presented to the Jardin d'Acclimatation. The receipt of "another nest" of *scutellaris* in an excellent state of preservation even though it was infested by innumerable mites was reported by Drory in 1875 (p. cxxxiv).

The principal provider of colonies was the indefatigable L. J. Brunet of Bahia, Brazil, who never tired of sending Drory fresh supplies of bees. But be it said in passing that Brunet's services were not merely those of a cooperative enthusiast strategically situated, who furnished others with material for study. He was also a contributor to the written record, for in the Bulletin de la Société d'Acclimatation (Raveret-Wattel, 1873b, p. 350) mention is made of a memoir that he produced on the Meliponidae of Brazil. In recognition presumably of his many services towards a better knowledge of stingless bees he was awarded a medal by the society. His thanks for this honor are recorded in the Bulletin for 1873 (Brunet, 1873b, p. 502), but even more significant is that with the thanks was coupled an announcement to the effect that a further shipment of 14 colonies was on the way.

Although Paris figures so largely in the stingless bee records of this period the suggestion that attempts be made to introduce meliponids into Algeria recurs again and again. Allusion has previously been made to the proposal with this end in view made by A. Poey. Another who pressed the recommendation was Hamet (1864b, p. 302), who was confident that *Melipona* was adapted for living in Algeria. Indeed such was the interest in France regarding the possible introduction of stingless bees into suitable new areas that at the General Session of the Société d'Acclimatation held June 7, 1872, there was appointed at the suggestion of Raveret-Wattel a committee consisting of Boisduval, Maurice Girard, Raveret-Wattel, and Thozet to investigate the possibility of establishing colonies of *Melipona* bees in France or in Algeria. Raveret-Wattel (1872b, p. 429) was eager to obtain for the guidance of the committee all possible information bearing upon stingless bees and was instrumental in having drawn up (1872c, pp. 430-432) a question-

naire directed to correspondents in countries where stingless bees occur covering many points helpful to the investigation. The committee expressed the opinion that an experimental introduction of stingless bees might be made in the Island of Reunion, at Senegal, and then in Algeria.

In the following year (1873) the answers to the questionnaire began to come in and in the Bulletin de la Société d'Acclimatation for that year are comments by Brunet (p. 260), by Voisin (pp. 260-261), by Salzedo (p. 353), by Thozet (p. 750). One has the feeling, however, that the response was somewhat scattered and therefore not wholly satisfactory. However, if scant, the replies in some cases at least had quality. In the annual report of the Société d'Acclimatation for 1873 Raveret-Wattel (1874, p. lxxxiii) was able to say: "Several of your correspondents have replied with particular care to the questionnaire which you have addressed to them concerning the Meliponidae or stingless bees, and some of the memoirs which have thus reached you furnish documents truly precious for the still far from completed history of these interesting insects."

An incentive to experiment with the acclimatization of stingless bees antedated the efforts of Raveret-Wattel and his committee. In 1870 a prize of 500 francs was offered to that individual who might succeed in maintaining an introduced colony of these bees in a living condition during two years [Bull. Soc. Imp. Zool. Acclim., vol. 17 (ser. 2, vol. 7), p. xxiii]. The contest was to run for 10 years, until 1880. Originally the bees were limited to those from America or Australia, but in 1876 the range of representation was widened to include also stingless bees of African origin. In 1881 the offer was extended to 1885, and a further extension to 1890 was established in 1886. There was no renewal of the offer in 1891 and presumably it was allowed to lapse. The fact that this prize was maintained for 20 years tends to emphasize the persistent hope of the donors that the experiment might succeed. Finally Pérez (1895a, p. 273) kept alive a colony for three years, but where is not indicated.

Belonging to the sixties is the record made by Cornelius (1875, pp. 184-185) of the receipt on July 16, 1869, of a New World

Trigona colony that unfortunately died out only a few days later, although there was a plentiful supply of honey still untapped in the provision pots. The species just mentioned appeared in the report of Cornelius under the name of *lineata*, and this name was likewise bestowed upon a colony that Tomaschek (1879, pp. 582-587; 1880, pp. 60-65) acquired. Both colonies were discovered accidentally in stems of *Haematoxylon campechianum* and were of Central American origin. Almost certainly, therefore, they were not *lineata*, which is probably not represented north of South America [see discussion of *Trigona* (*Paratrigona*) *lineata* var. *lineata* (Lepeletier), p. 363]. Although the colony of Cornelius succumbed soon after it came into his possession, the colony acquired by Tomaschek flourished until at least well into the fall, thanks to the precaution taken of placing the hive indoors at the approach of cold. Yet another colony that was ascribed to *lineata*, and in this instance indubitably not *lineata*, was obtained, likewise in "Campeche wood," from Yucatan (Du Buysson, 1901a, p. 106; 1901b, p. 155). This colony lived for several months at the laboratory of entomology, in Paris, but died out at the end of winter.

Another species that towards the end of the summer of 1900 enjoyed the alien hospitality of the laboratory of entomology was *Melipona beecheii* E. T. Bennett, received from the State of Jalisco, Mexico. The bees expired with the first cold spell after having devoured the stores of honey in their nest (Du Buysson, 1901a, pp. 104-106; 1901b, pp. 153-156).

In spite of devoted care bestowed by H. Müller (1875a, pp. 80-82; 1875b, pp. 41-55) a colony of *Trigona* (*Tetragona*) *jaty* F. Smith received from Brazil and installed at Lippstadt, Germany, ultimately succumbed on November 28 after having been maintained for four months. In all likelihood it would have succumbed before that time, however, had not Müller at the end of October transferred it to his living room. In spite of the unhappy outcome of this attempt at acclimatization, Müller held to the opinion that the chances of successfully maintaining a colony over winter were greater than the chances of failure and urged zoological gardens to make the attempt, and to spare neither expense nor

labor in the effort. Yet another colony of *jaty* survived the crossing of the Atlantic, finally reaching the Hamburg Museum in 1895.

It was a nest of *Melipona quinquefasciata* Lepeletier, a species known from Brazil and Argentina, that, established as a living colony in Germany during the summer months and persisting beyond the middle of September, furnished Dreyling (1905, pp. 315-322) with the material for his studies on the wax producing glands of Meliponidae.

Several attempts were made to establish stingless bees in the United States. In the spring of 1886 the inventor of the bee-smoker, T. F. Bingham, brought a colony from Mexico and set it up in Michigan, but the northern climate proved disastrous and the bees succumbed in the fall of the same year (Dadant and Dadant, 1889, p. 290; Cook, 1902, p. 40).

"Various specimen lots of the stingless bees" were sent by W. K. Morrison to Stephen N. Green, who published an article regarding them (1905, pp. 1315-1318) in which he claimed virtues for them not possessed by the honeybee and expressed the hope that, with fuller knowledge regarding them, it might be possible to carry them successfully through a northern winter, a hope that seems rather remote.

Two colonies of stingless bees were brought from a point 300 miles up the Orinoco River to Jenkintown, Pennsylvania, likewise by W. K. Morrison, where in a public demonstration in 1906 he unwittingly proved to the joy and excitement of the assembled spectators that even stingless bees can prove distressingly annoying (E. R. Root, 1906, pp. 1061-1064).

In 1907 still another nest with about 300 living occupants was brought from the interior of Venezuela by the same indefatigable Morrison and was installed through the courtesy of A. I. Root Company in the American Museum of Natural History, where, it is said, people were able to view the habitation and the out-going and in-going bees through the glass-covered box that housed the colony. The incident is no longer remembered within the Museum, but the explanation given in a pertinent article (Harding, 1907a, pp. 5-9; 1907c, pp. 693-694) was

to the effect that "The visitors were brought to the United States with the idea that they might be crossed with the honey bees and a new stingless species thus produced combining this advantage with the superior qualities of the native insects." This chimerical suggestion arises again and again but would seem utterly impracticable. One is, therefore, glad to add Harding's further comment (1907a, p. 5; 1907c, p. 693): "The species (Stingless bee and *Apis*) were so remotely related and the habits of the stingless variety so highly specialized, however, that the scientist at the museum considered hybridization to be an impossibility."

Many stingless bees have arrived in foreign parts accidentally or have been acquired with a view to the study of their habits, but there was discussion at one time of attempting their introduction into the United States solely in the interests of pollination (Cook, 1905, p. 631; Phillips, 1905, p. 679). Partly this was based on the impression expressed by Cook that "cross-pollination will be more generally affected with every increase of species of bee among us." But Harding (1907a, p. 5; 1907c, pp. 693-694) went even further than Cook and stated that as pollen gatherers stingless bees are "vastly superior" to the honeybee, "being able to carry much heavier loads and to work longer and in weather when the honey bee would not venture out." The claim that the loads are heavier needs painstaking rechecking. It cannot be applied generally.

Not only from the New World but from the Old World, too, nests of stingless bees have reached Europe. Waterhouse (1903, pp. 133-136, pl. 6) received from Malacca a nest that he ascribed to *collina* (but which I have interpreted as typical *Trigona apicalis* F. Smith) and from Singapore a nest that he referred to as *ruficornis*. In both cases the occupants of the nest survived the long sea voyage. A nest of what Schulz (1909, pp. 338-341) referred to as *Trigona canifrons* F. Smith [more likely it was that of *Trigona (Tetragona) iridipennis* F. Smith] was received from Java, and its inmates were kept alive at Paderborn, Germany, until early November, when the first night of frost proved fatal.

The instances cited thus far have included isolated attempts to acclimatize in temperate

regions creatures of the tropics that either through accidental transportation or with deliberate intent were shipped to regions ill suited to their constitution. Repeatedly we have seen that, even though they survived the ocean trip and might come through the warmer months of the year successfully, cold weather was fatal to them in the end. Of all of those interested in maintaining under alien conditions an apifauna unused to frosts and snow none, however, can compare with Edouard Drory in his deliberate and persistent attempts to surround himself with colonies of these exotic bees. On his place in Bordeaux, more suitable climatically for the maintenance of Meliponidae than any of the other destinations in Europe to which fate consigned them, he had at one time (1873) no fewer than 21 different colonies belonging to 11 different species, all obtained through the friendly cooperation of L. J. Brunet of Bahia, Brazil, to whom great credit is due for gathering such abundant material and placing it in the hands of one who could make such good observational use of it (Drory, 1874, p. 281). In the following year (1874) eight additional colonies arrived, while as early as 1871 and 1872 initial attempts had been made by Drory to establish stingless bee colonies in Bordeaux.

His early material consisted of colonies of *Melipona fasciata* variety *scutellaris* Latreille. By 1874 he had received no fewer than nine colonies of this bee, which figured importantly in his investigations; eight of these had reached him in a living state. We may again express wonder at the toughness and endurance of these bees that in the early seventies, when crossings were slow, maintained themselves through all the vicissitudes of the long journey.

Yet, successful in reaching a distant shore, the bees could not survive the winter in Bordeaux. At least, most of them succumbed. Two colonies out of a total of 21 managed to persist through the cold months of 1873-1874, but in April one of these two colonies [referred to as *calipes* by Drory but to be interpreted possibly as *Trigona (Tetragona) nigra* variety *paupera* (Provancher)] succumbed to an attack of ants. The other of the two colonies that survived the winter of 1873-1874, referred by Drory to *Melipona*

inhati mirim and described by him as the smallest species of all, was still living when Drory prepared his paper (1874, pp. 281-286) for delivery before the September gathering of German and Austrian apiculturists in Halle, but the colony in question was by that time very weak.

Stingless bees do not cluster as does the honeybee and hence do not generate the needed heat to survive. To work actively within the nest a temperature of 30° C. is desirable; at 25° the activities of the bees are already susceptible to a notable decline. Drory found that at 18° the stingless bees would fly forth only in very small number, at 15° not at all, while 10° was fatal to them. On the other hand, the higher the temperatures in Bordeaux, the more lively they became, the more they worked, the happier they seemed to be (Raveret-Wattel, 1872d, p. 688; Drory, 1877, pp. 148-149). Drory noted that the queen is one of the very last, if not the last, to perish (1877, p. 115, footnote). Tomaschek (1880, p. 64) kept his *Trigona* colony in a room, the mean temperature of which was about 14° C., but took the

precaution of introducing into the nest twice a day a vessel containing water with a temperature of 40° C. so as to raise the temperature of the nest. Rather closely in accord with Drory's observations are those of Rayment (1932, p. 247), who found that, when the outside temperature descends to 12° C., such Australian stingless bees as *Trigona carbonaria* F. Smith and *Trigona cassiae* Cockerell no longer leave the hive. At 10° they crawl slowly over the combs and do not take wing. Before dismissing this subject, mention should be made that at 20° C. von Buttel-Reepen (1907, p. 468) found *Trigona* (*Plebeia*) *emerina* Friese "surprisingly lively, capable, and feverishly active."

The attempts at acclimatization of stingless bees have not proved a success, and yet the fact that in some instances, with favorable environment, colonies have been maintained for a time gives substance to the hopes that H. Müller expressed with respect to the installation of colonies for the interest that they would awaken among those who have never seen stingless bees engaged in their activities.

SYSTEMATIC ACCOUNT

SUBGENERA, SPECIES, AND VARIETIES

THROUGHOUT THIS PAPER the attempt has been made not only to indicate relationships of different species by grouping them into subgenera but also to place in the same species forms that, while differing in their maculations, basic color, color of hairs, etc., are nevertheless from a structural standpoint either identical or so essentially alike that one is tempted to interpret them as being fundamentally one. In my paper on *Melipona* (1932a, pp. 231-460, pls. 1-10) I gave to populations that differed from the typical representative of the species the rank of subspecies, and in some ways such a designation seems preferable to the more old-fashioned word variety employed in the present monograph. In many cases what are here designated varieties will doubtless prove to be subspecies. Nevertheless I have taken refuge in the term variety because it is somewhat more vague and noncommittal than subspecies and hence does not carry implications that may ultimately prove in some cases to be unjustified. It is indeed difficult in the present state of our knowledge to be too positive regarding the category to which to assign a given stingless bee. Sometimes, owing to paucity of material, it is almost impossible to say whether a particular variant belongs to a subspecies in the sense of a geographic race or is merely a member of an aberrant population in a species that shows great instability of coloration. Reinig (1939, Zool. Anz., Supplement, vol. 12, p. 174) summarized the bumblebees as consisting of 300 species, 1200 geographic races or subspecies, and 1500 individual variants, and it would seem not unlikely that in the stingless bees, too, geographical races and individual variants are both abundantly represented.

In some cases [for instance, that of *Trigona* (*Trigona*) *trinidensis* variety *silvestriana* Vachal] one can say with confidence that at the least a geographic race is involved; but in other instances [for example, the several varieties of *Trigona* (*Parapartamona*) *zonata*] the differences noted may be merely those of individual nest populations or of microsubspecies, an interpretation strengthened by the fact that all of the members of *Parapartamona* herein described occur within Colombia and Ecuador. How complicated the question of interpretation may become is illustrated in the bumblebees by a species like *Bombus ruderarius*, which is represented by eight types of variation in the environment of Riga, reduced to five or six types of variation in Sylt, reduced still further to three or four in Brandenburg, to two or three in Frankland, and peters out to a single variant in Belgium, England, and the Balkan peninsula (Reinig, 1939, *ibid.*, p. 182). A great deal more collecting will have to be done before such gradations of variability can be offered for members of the genus *Trigona*, but the variability of the maculations in a subgenus like *Paratrigona* suggests that a profitable beginning might be made in that group. The day is probably still distant when the stingless bees can be elucidated as to species and subspecies with the degree of precision already possible in the case of the birds. Meanwhile, under the stimulus of works such as "Systematics and the origin of species" by Ernst Mayr (1942), those who study the stingless bees as well as other groups of insects will probably be prompted to do their part in extending the knowledge of infra-specific categories and thus further an understanding of the ramifications of life.

GEOGRAPHIC DISTRIBUTION AND PLACE NAMES

In this changeable world even geographical names are impermanent. Happily, within the area here covered, there have been no such drastic substitutions of new names for established names as have accompanied political changes and redrawing of boundaries in the

Old World. Nevertheless, changes have occurred even in the American tropics while this monograph has been in course of preparation. In Brazil in particular there has been revision of the old names, and not a few localities today appear under altered design-

nations. After weighing the pros and cons the decision has been reached to abide by the old nomenclature. Many of the new names are sufficiently like the old to obviate confusion, but even more potent in influencing the retention of the old names has been the circumstance that these names are predominantly in accord with the localities indicated on the labels attached to the specimens and thus facilitate the task of anyone who may

have occasion to recheck the material on which this study is based. The retention of the old names has been observed even in those cases where, owing to boundary adjustments, a given locality is today incorporated in a country to which at the time the specimen was collected that locality did not belong. Especially is this true of certain Colombian localities at one time credited to Peru, namely, those of the Putumayo District.

MEASUREMENTS

Comparative estimates of size—such as the distance separating the compound eyes at their level of greatest convergence (below) as contrasted with their divergence at a level just below the anterior ocellus, and like comparisons of other parts—have been arrived at through the use of a cross-hatched micrometer eyepiece. It is in order to state that without this aid (that is, if the insect be viewed through a microscope unprovided with such a reticulated scale) the relationship in size of one part to another is apt to be distorted by the character of the surface, a surface of even slightly arched character unconsciously being interpreted as of somewhat greater extent linearly than is actually the case. But in any event the measurements are hard to record with accuracy owing to the fact that the slightest inclination of the specimen from the horizontal will affect the interpretation and distort the comparative estimate.

The larger measurements (length of bee, thoracic width, and length of forewing) have been made by means of a caliper with millimeter scale attached.

KEYS TO THE GENERA AND SUBGENERA OF NEW WORLD STINGLESS BEES

WORKERS

1. Joint 3 of the antennae nearly as long as joints 4+5. The upper half of the head strongly convex in profile. The labrum with two strong tubercles and a pronounced median depression. The malar space relatively long, at its shortest part at least as long as the flagellum is wide. The clypeus very short, only about one-third as long as wide. Head not merely wide but thick, the genal area (beyond the outer orbit of the eyes) having a

width greater than that of the compound eyes. The outer face of the hind tibiae of rather uniform surface, nearly flat throughout, with the apical part of this face unmodified, not depressed; the anterior lateral contour as well as the posterior of these tibiae convex, the hairs fringing them simple (not plumose). No tibial comb anteriorly at the apex of the hind tibiae

. *Lestrimelitta* Friese

- Joint 3 shorter, usually conspicuously shorter, than joints 4+5. The outer face of the hind tibiae either more flattened at the apex than towards the base, or more or less depressed or excavated at the apex, and in some species with an excavation extending from the apex almost to the base. A tibial comb anteriorly at the apex of the hind tibiae 2.
2. Stigma poorly developed, rather narrow and linear, tending sometimes to be slightly concave along its apical half or tapering to a point apically, not rounded below. Wings relatively short, not or (exceptionally) barely extending beyond the apex of the abdomen. Number of hamuli per lower wing in no species averaging below nine, although exceptionally an occasional individual may have as few as eight hamuli; range usually between nine and 16 hamuli. Propodeum as a rule densely tessellated. The hind tibiae of an elongate triangular shape, the outer apical angle definite and down-pointing or out-pointing, not rounded or with the angle inwardly placed. Robust. Length, 6 to 13.5 mm. . . . *Melipona* Illiger
- Stigma more fully developed, rounded below. Wings relatively long, extending well beyond the apex of the abdomen. Number of hamuli per lower wing in none of the New World species averaging as high as nine hamuli, although in one or two species (*quadripunctata* and *capitata*) there are individuals that have as many as nine or even

- 10 hamuli per lower wing; range usually between four and eight hamuli. Body length rarely more than 8 mm., very exceptionally as much as 11 mm., in the great majority of cases under 8 mm., grading down to species in which the length is about 2 mm. *Trigona* Jurine . . . 3
3. Exceedingly small bees, ranging from around 2 mm. in length to around 4 mm. The head always without a stripe extending part way or continuously along the inner orbit of the eye; the mesonotum in only one species (*schrottkyi*),¹ which is densely tessellated on head and thorax, with a stripe along its lateral borders. The apex of mandible not toothed from end to end. The malar space usually well developed (*schrottkyi* is an exception). The head and thorax often tessellated, more rarely smooth. The propodeum in dorsal aspect long compared to the scutellum. The hairs fringing the posterior lateral contour of the subtriangular to clavate hind tibiae simple (unbranched), silvery gray, and in some species very long. The marginal cell in certain species semi-open or very imperfectly closed, the apical one-third or one-fourth of the marginal vein being in such cases vestigial to absent. When the apical part of the marginal vein is not so extensively vestigial, then the posterior lateral margin of the hind tibiae is usually more or less minutely serrate, a character shared also in varying degree by certain of the species that have an obsolescent marginal vein. The stigma relatively long (from one-half to two-thirds the length of the marginal cell), frequently of a watery to slightly yellowish transparency, or opaque whitish to pale yellowish, more rarely brownish. The abdomen of approximately the same width as the thorax *Trigona* subgenus *Hypotrigona* Cockerell
- For the most part larger bees. When of comparable size to *Hypotrigona*, then either with stripes along at least part of the inner orbit of the eye (and also margining the mesonotum) or with the abdomen long and narrow, conspicuously narrower than the thorax 4
4. The head (lower half of face in some species excepted) and thorax entirely smooth and polished or with sculpturing so sparse and delicate that the shininess of the surface is usually dulled, if at all, only by the presence of hairs 5
- At least the thorax and usually also the head with clearly defined sculpturing: tessellate, rugosely pitted, punctate, granular, or a combination of these 10
5. The mandible toothed usually from end to end along its apex, or with three teeth on at least the outer half or two-thirds of the apex and an angulation at the inner extremity, the teeth usually clearly separated but sometimes with thin septa of chitin connecting them. The hind tibiae a little longer than the combined length of their femora and trochanters. The fringe along the posterior lateral contour of the hind tibiae with plumose hairs in addition to the usually sparser simple hairs. The base of the inner face of the hind metatarsi with a differentiated, more or less oval area of appressed hairs that contrast with the brush-like hairs on the apical one-half to two-thirds of this inner face *Trigona* subgenus *Trigona* Jurine
- The mandible with the outer half, at least, of the apex edentate. The inner face of the hind metatarsi almost invariably (at least in the case of the Neotropical species) with bristles basally as well as apically on the inner face of the hind metatarsi (the very few exceptions belong to the subgenus *Tetragona*) 6
6. The head abnormally wide and short. The clypeus small and very remote from the rather diminutive eyes, densely if finely tessellate to punctate (as are also usually the adjacent regions of the sides of the face) and of somewhat irregular surface, often slightly swollen over the middle region of the clypeus with sometimes a complete or incomplete median longitudinal fossa bisecting the swelling. The malar space rather exceptionally long, fully one and one-half times to twice as long as the flagellum is wide. The hind tibiae subtriangular, with a tooth-like angulation posteriorly at the apex *Trigona* subgenus *Oxytrigona* Cockerell
- Not having this combination of characters. 7
7. The hind tibiae greatly expanded, about one-half as wide as long, their exterior face deeply hollowed from the apex almost to the base, a little suggesting the bowl of a spoon, the anterior lateral contour being almost as convex as the posterior lateral contour and both of these contours fringed with rather eyelash-like, moderately long simple hairs. The dorsal and middle region of the propodeum as well as the sides of the propodeum usually hairy. The clypeus usu-

¹ Moure (1946a, p. 441) has erected the genus *Friesella* to accommodate *schrottkyi*.

ally with an L-shaped maculation backed by an L-shaped maculation in reverse, but these maculations sometimes consolidated and in other cases fragmentary or all but obliterated¹

. . . *Trigona* subgenus *Partamona* Schwarz
The hind tibiae of different shape and lacking so extensive a corbiculum. The dorsal and middle region of the propodeum as a rule bare. The clypeal maculations, if present, of other than L-shape 8

8. The hind metatarsi conspicuously wide, slightly wider than the hind tibiae and greatly thickened, with a distinctly swollen appearance. The hairs fringing the posterior lateral contour of the almost triangular hind tibiae very short

. . . *Trigona* subgenus *Scaura* Schwarz
The hind metatarsi not so wide as their tibiae, their outer face usually more or less flat . 9

9. The inner face of the hind tibiae unevenly gabled but with a sharply elevated, median, plateau-like area that extends from the base almost to the apex and contrasts strongly with a flat, wide, posterior rim (particularly widened at the apex). The contour of the hind tibiae more or less clavate with the apex in all cases much wider than the base and sometimes conspicuously expanded. Plumose hairs in addition to simple hairs usually present along the posterior lateral contour of the hind tibiae or present over their outer face near the base or both . . *Trigona* subgenus *Tetragona* Lepeletier²

¹ It is possible to confuse such specimens of obscure maculation of the clypeus with the closely related but rare subgenus *Parapartamona* (see end of this key) in which the clypeus lacks maculations but the sides of the face in contrast are richly ornamented. Aside from the fact that such a contrast is unusual in *Partamona*, the subgenus *Parapartamona* has eyes that are more convergent below than the nearly subparallel eyes of *Partamona*, its mesonotum is at least lightly tessellated rather than smooth, its propodeum is nearly twice as long as its scutellum, and its hind tibiae, while deeply excavated, are narrower than those of *Partamona*.

² In a paper entitled "Abelhas de Batatais," Moure (1943, p. 146) erects from material here still tentatively retained in *Tetragona* another subgenus, *Geotrigona*. In a key, which I was privileged to read and which, it is to be hoped, may soon be published, he differentiates between his new subgenus and *Tetragona* as follows:

"5. Thorax and abdomen elongate, the latter narrow with the dorsal surface more or less obtusely angled; hind tibiae neither clavate or club-shaped (Genotype: *clavipes*)

. *Tetragona* Lep. et Serv., 1825.
Thorax and abdomen rather short, the latter broad and with dorsal surface slightly convex; hind

The inner face of the hind tibiae unevenly gabled but the backward-sloping and longer plane bordered by only the narrowest of posterior rims or none at all. The contour of the hind tibiae subtriangular to slightly clavate. Only simple hairs bordering the posterior lateral contour of the hind tibiae *Trigona* subgenus *Plebeia* Schwarz

10. The tessellated upper part of the head and the tessellated mesonotum metallic blue . . .

. . *Trigona* subgenus *Mourella* Schwarz
The head, thorax, legs, and abdomen without metallic coloration 11

11. A large prominent tooth at the inner extremity of the otherwise edentate mandible. The clypeus, lower part of supraclipeus, and lower extremity of sides of face coarsely punctured but shiny in contrast to the densely granular and dull upper half of the head. The hind tibiae wide, almost one-half as wide as long and rather deeply but also somewhat irregularly hollowed.

. *Trigona* subgenus *Cephalotrigona* Schwarz
Not having this combination of characters 12

12. The base of the scutellum with a shiny V-shaped to U-shaped emargination at its middle 13

The scutellum without an emargination at its base 14

13. The scutellum with an apical emargination. Malar space short, not so long as, or no longer than, the flagellum is wide. Tergites 1 and 2 of the abdomen proper largely polished, the concavity at the base of tergite 1 not distinctly separated from the dorsal part of the tergite

. *Trigona* subgenus *Nannotrigona* Cockerell

The scutellum with its posterior margin rounded and entire. The malar space long, distinctly longer than the flagellum is wide. Tergites 1 and 2 of the abdomen more or less densely sculptured, frequently granular and opaque, the polished basal concavity of tergite 1 clearly demarked from the sculptured dorsal part of the tergite by a carina . . *Trigona* subgenus *Scaptotrigona* Moure

14. The mandibles more or less distinctly quadridentate along their apex, but the dentition sometimes obscured by intervening septa of chitin. The head and thorax densely and finely granular (like the striking surface of a matchbox); the facial quadrangle notably longer than wide; a stripe at least along the

tibiae not club-shaped, with the posterior contours moderately convex (Genotype: *mombuca*) *Geotrigona*, new."

inner orbit of the eye and often along lateral margin of mesonotum. The scutellum extended backward, slightly or largely over-roofing the propodeum. The hind tibiae subtriangular to clavate with their outer face depressed only towards the apex posteriorly

. . . *Trigona* subgenus *Paratrigona* Schwarz

The mandibles with the inner one-third of their apex armed with two denticles but the outer two-thirds edentate. The sculpturing on head and thorax fine to very fine; at least the mesonotum without bordering stripes. The scutellum not extended backward over the propodeum. The outer face of the hind tibiae with a shallow or deep depression that is not confined to the apex but occupies virtually the entire expanse of the rather wide joint from the apex almost to the base, a little suggesting the bowl of a spoon because the anterior lateral contour of the joint, as well as posterior lateral contour, is rather convex. 15

15. The side-facial maculations not extending upward beyond the maculated clypeus. The malar space shorter than the flagellum is wide. The mesonotum finely tessellated. The propodeum in dorsal aspect barely longer than the scutellum and distinctly tessellated. The depression occupying the outer face of the hind tibiae rather shallow. The first discoidal cell barely shorter than the marginal. Number of hamuli per lower wing seven to nine

. . . *Trigona* subgenus *Schwarziana* Moure

The side-facial maculations extending upward almost to the level of the ocelli. The clypeus immaculate. The malar space longer than the flagellum is wide. The mesonotum very finely tessellated. The propodeum in dorsal aspect about twice as long as the scutellum. The depression occupying the outer face of the hind tibiae very deep. The first discoidal cell only about two-thirds as long as marginal cell. Number of hamuli per lower wing usually five . . . *Trigona* subgenus *Parapartamona*, new subgenus

QUEENS

(No key is offered for the queens of the different subgenera of *Trigona* because the fragmentary knowledge of this caste makes it difficult to arrive at a trustworthy generalization of the subgeneric characters.

Judging from the limited number of queens of the subgenus *Trigona* that are known, the queen of this subgenus may, like the worker, be sepa-

rated from other subgenera of smooth chitin by the fact that the apex of its mandible is toothed from end to end although more obscurely so than is the case in the worker.

Similarly, the only example I have seen of a queen of *Paratrigona* had the mandible completely toothed. Perhaps this character can be relied upon to separate the queens of this subgenus from the queens of other subgenera of sculptured chitin. But Ducke (1916, p. 105; 1925, p. 400; 1945, p. 80) says nothing about the dentition of the mandible in his brief description of the queen of *lineata*, a member of *Paratrigona*, and as the dentition is often obscure in the worker, perhaps it is obscure to obliterated in some instances also in the queen.)

1. Joint 3 of the antennae notably longer than 4 and not a great deal shorter than 4+5. The upper half of the head strongly convex in profile. The clypeus very short, about three times as wide at its widest as it is long. The labrum with a tubercle-like raised area on each of its lateral edges. The genal area very notably wider than the small parallel compound eyes. The outer face of the hind tibiae rather flat and shiny (largely to wholly devoid of hairs); the anterior contour distinctly convex, more convex than the fringed posterior lateral contour. *Lestrimelitta* Friese
Otherwise 2
2. Stigma poorly developed, rather narrow and linear, tending sometimes to be slightly concave below along its apical half or tapering to a point apically, not rounded below. The virgin queen of slightly smaller stature, at any rate no larger, than the worker
. *Melipona* Illiger
Stigma more fully developed, rounded below. The queen of larger stature, with a notably wider thorax, than the worker
. *Trigona* Jurine

MALES

(Many species of stingless bees are known only from the worker, and the key that follows may well fail, therefore, to apply to all of the species which on the basis of the worker have been assigned to different subgenera of *Trigona*. The key is at best tentative, and three subgenera of *Trigona*—*Mourella*, *Parapartamona*, and *Hypotrigona*—are not included. The males of the first two subgenera are unknown, and there are before me no males of the third subgenus, the male of only a single species of which has been reported.

Alone among the New World Meliponidae the worker, at least, of *Mourella* is metallic colored; it is perhaps not too venturesome to conclude that the unknown male of this subgenus, when discovered, will prove to be of similar distinctive

coloration. However, certain ants of the genera *Macromischa* and *Rhytidoponera*, the workers of which are metallic colored, have males that are uniformly red, yellow, black, or brown. So one cannot be certain. Regarding the unknown male of *Parapartamona* it is unwise to speculate, but the worker is so distinctive that very likely the male, too, will share some of this distinctiveness. Size and wing characters will probably help in placing the unknown male of some of the species of *Hypotrigona* (see in this connection the key to the workers above). Ducke's description (1916, p. 88; 1925, p. 360; 1945, p. 68) of the male of *muelleri*, the only *Hypotrigona* of which the male is recorded, is too brief to be of value.

It is hoped that the following key, in spite of its inadequate basis, may prove of some help in identifying isolated male specimens as to subgenus. Where male specimens are accompanied by workers, the key for the workers will doubtless prove more reliable.)

1. The fourth antennal joint viewed from below only a little longer than the third; viewed from above, barely shorter than the third. Labrum with a tubercle, even if sometimes feeble, at each lateral extremity and a more or less depressed area between. Clypeus very short, less than one-half as long as it is wide. The anterior lateral contour of the hind tibiae more convex, if anything, than the posterior lateral contour. *Lestrimeliitta* Friese
Not having this combination of characters.
The fourth antennal joint viewed from below usually at least double and frequently several times the length of the third antennal joint 2
2. Stigma poorly developed, rather narrow and linear, tending to be slightly emarginate below along its apical half or tapering to a point apically, not rounded below. Wings relatively short, not or (exceptionally) barely extending beyond the apex of the abdomen. Number of hamuli per lower wing ranging from nine to 15, with an average above nine in all species. Propodeum as a rule densely tessellated. Robust *Melipona* Illiger
Stigma more fully developed, rounded below. Wings relatively long, extending well beyond the apex of the abdomen. Number of hamuli per lower wing usually five or six, in only two New World species (*quadripunctata* and *capitata*) ranging from seven to nine or even 10, but even in these species with an average of under nine *Trigona* Jurine . . . 3
3. The inner face of the hind tibiae unevenly

gabled but with a more or less distinctly elevated median plateau-like area that extends from the base almost to the apex and contrasts, often strongly, with the more flattened area posterior to it, which is widest near the apex 4

- The inner face of the hind tibiae likewise unevenly gabled but the backward sloping and longer plane without distinctions of elevation, its slanting surface terminated only at approximately the posterior contour of the joint, a distinct posterior rim being wanting 6
4. The head, thorax, and abdomen with fine, dense, granular sculpturing. Mandibles (relatively wide apically, but narrower than along the base), labrum (faintly bituberculate), clypeus, supraclypeus, and scape brightly maculated, but no, or scarcely any, maculation on the sides of the face. The hairs on the external face of the hind tibiae and along the anterior and posterior lateral contours of these tibiae simple (unbranched). Sternite 6 armed at its apical middle with a rather wide tooth (this tooth nearly as wide as long and sometimes even wider than long) with its apex approximately as wide as its base and subtruncate except for a tiny nipple-like projection at the middle
 Trigona subgenus *Cephalotrigona* Schwarz
The head, thorax, and abdomen wholly or virtually wholly smooth and sculptureless. The hind tibiae in many but not in all species with branched hairs on their outer face or along their posterior lateral contour. Sternite 6 armed at the middle of its apex with a rather long spine that usually tapers to a point; in the rare case when this median armature is widely tooth-like rather than spine-like, then at least the apex is not approximately truncate but acutely pointed. 5
5. The hind metatarsus with an oval or suboval area of appressed sericeous hairs at the base of the inner face, contrasting with the more bristle-like hairs apical thereto. The face without ornamental maculations.
 Trigona subgenus *Trigona* Jurine
The hind metatarsus in all known males of New World species without such a differentiated area. The face frequently maculated
 Trigona subgenus *Tetragona* Lepeletier
6. The head (lower half of face in some species excepted) and the thorax entirely smooth and polished or with sculpturing so sparse and delicate that the shininess of the surface is usually dulled, if at all, only by the pres-

- ence of hairs 7
- At least the thorax and usually also the head with clearly defined sculpturing: tessellate, punctate, rugosely pitted, or a combination of these. 10
7. The head rather exceptionally wide and short. The clypeus small and rather remote from the eye, its greatest width only a trifle more than its length, finely but rather densely tessellate to punctate (as are also usually the adjacent regions of the sides of the face). The malar space clearly demarcated. A rather long spine at the middle of the apex of sternite 6
- . . . *Trigona* subgenus *Oxytrigona* Cockerell
- Not having this combination of characters . 8
8. Frequently an L-shaped maculation backed by a reverse L-shaped maculation on the clypeus, or these maculations coalescent or fragmentary, rarely wholly absent. Hair, even if thin, usually present on the dorsal and middle region of the propodeum, not confined merely to the sides. The middle of the apex of sternite 6 armed with a strong spine
- . . . *Trigona* subgenus *Partamona* Schwarz
- Clypeal maculations, when present, of different character. The dorsal area of the propodeum bare 9
9. The hind metatarsi distinctly narrower than the hind tibiae. Facial maculations usually present. Sternite 5 with two more or less triangular to spine-like lateral elements separated from each other by a deep median emargination. Sternite 6 with the central apical spine usually relatively short, usually shorter, or at any rate no longer, than the lateral "shoulders," sometimes even absent
- . . . *Trigona* subgenus *Plebeia* Schwarz
- The hind metatarsi fully as wide as their tibiae and distinctly swollen over their external face. Facial maculations absent. Sternite 5 only briefly emarginate at the middle, the lateral elements not widely or nearly completely separated from each other and not subtriangular or spine-like in contour. Sternite 6 with a strong median spine. The minute sternite 7 subrectangular with a relatively long spine at its apical middle . . . *Trigona* subgenus *Scaura* Schwarz
10. The base of the scutellum with a small, usually shiny, V-shaped or U-shaped emargination at its middle. Often without or nearly without facial maculations 11
- The scutellum without an emargination at its base. At least the lower half of the head (and usually more of the head) conspicuously maculated. The sculpturing dense but

- exceedingly fine, never coarsely rugose or scattered 12
11. The scutellum with an apical emargination. Tergites 1 and 2 of the abdomen proper largely polished, the concavity at the base of tergite 1 not distinctly separated from the dorsal part of the tergite
- . . . *Trigona* subgenus *Nannotrigona* Cockerell
- The scutellum with its posterior margin rounded and entire. Tergites 1 and 2 of the abdomen proper more or less densely sculptured, frequently granular and opaque, the polished basal concavity of tergite 1 clearly demarcated from the sculptured dorsal part of the tergite by a carina
- . . . *Trigona* subgenus *Scaptotrigona* Moure
12. Facial maculation confined to the lower one-half of the face. The head and thorax with abundant erect hairs. Sternite 3 with a conspicuous crescentic fimbria of erect hairs that arches about an area of dense, soft, plush-like tomentum apical to it
- . . . *Trigona* subgenus *Schwarziana* Moure
- Side-facial maculations, at least, extending to the upper half of the head. At least the face and mesonotum and usually other parts of the head and thorax as well with few or no erect hairs, although with a sericeous sheen. No crescentic fimbria on sternite 3
- . . . *Trigona* subgenus *Paratrigona* Schwarz

LESTRIMELITTA (FRIESE)

Trigona (*Lestrimelitta*) FRIESE, 1903, p. 361.

TYPE SPECIES: *Trigona limão* F. Smith.

WORKER

DIAGNOSTIC CHARACTERS: Especially differentiated by the following combination of characters: Upper half of head pronouncedly convex viewed in profile. The postorbital region of the head much developed, the genal area distinctly wider than the rather narrow eyes. The clypeus very short, only about one-third as long as wide. The labrum strongly bituberculate. The malar space fairly large, at its shortest part at least as long as the flagellum is wide. Joint 3 of the antennae (joint 2 of the flagellum) approximating in length joints 4+5 (this is true of the New World *Lestrimelitta* but does not apply to the African *cubiceps*). The anterior lateral contour of the hind tibiae convex; the outer face of these tibiae of rather uniform surface, the apical part of this face not depressed; the hairs fringing the anterior and posterior lat-

eral contours of these tibiae simple (not plumose).

HEAD (FIGS. 3A AND 7A): Somewhat wider than long in the New World species (subequal in length and width in the African *cubiceps*). The facial quadrangle wide, the distance between the eyes at a level just below the anterior ocellus about equal to the distance from the middle ocellus to the apex of the clypeus. The eyes parallel sided and relatively small and narrow (distinctly narrower than the wide genal area). The clypeus about three times as wide at its widest as it is long; its sides strongly divergent almost from the base to the apex; its apico-lateral extremities form a strongly acute angle; its apex is widely truncate along the middle with only a very feeble recession towards each of its extremities. The clypeus (in the New World species at least) is raised very slightly above the level of the sides of the face, its apex at the middle widely and moderately to very emphatically foveate. The mandibles overlapping, wider (but only a very little wider) at the base than at the apex, the outer two-thirds of their apex edentate, the inner one-third armed with two very diminutive and inconspicuous denticles that are sometimes hard to distinguish. The malar space well developed, at its shortest (towards the inner extremity of the base of the mandible) about one and one-half times as long as the flagellum is wide. The labrum strongly bituberculate. The supraclypeus (in the New World species) hardly more prominent than the upper half of the clypeus, subtriangular in contour, a little longer than wide, its more or less carinated summit connected with the middle ocellus by a shallow fossa. The middle ocellus barely anterior to the lateral ocelli, somewhat depressed, sometimes round but in other instances with its transverse axis greater than its longitudinal. The lateral ocelli very slightly tilted, each towards the nearest compound eye. The distance between the lateral ocelli distinctly less than that which separates each lateral ocellus from the nearest compound eye. A blunt low swelling behind the ocelli and coextensive with them. The lateral ocelli separated from the posterior edge of the vertex by rather more than twice their diameter. The head either nearly devoid of hairs or, if hairs be present, then the hairs

short even if dense. The antennae short; scape about three-fifths as long as flagellum; the second joint of the flagellum approximating in length the combined third and fourth joints (this is true, at least, of the New World *Lestrimelitta*).

THORAX: Either devoid of sculpturing or lightly tessellated according to the species. The mesonotum, measured at its widest near the base, almost as wide as the combined mesonotum and scutellum are long. The scutellum rounded over its posterior contour and entire (not emarginate) and barely or not at all impinging upon the hairless dorsal or middle region of the propodeum, which is shiny. The dorsal region of the propodeum, viewed from above, a little shorter than the scutellum. The thorax either for the most part without erect hairs, these being confined largely to the scutellum and the base of the mesonotum, or rather densely hairy over all but the dorsal and middle region of the propodeum.

LEGS (FIGS. 3B AND 7B): Progressively longer from the fore pair to the hind pair, the hind pair shorter than the length of the head, thorax, and abdomen combined. The tibiae of the fore legs notably shorter than their femora; those of the middle legs a little shorter than their femora; those of the hind legs longer than their femora but not so long as the combined length of their femora and trochanters. The hind tibiae (figs. 3B and 7B) elongate oval in outline, their posterior and particularly their anterior lateral contour more or less convex, with the result that the joint tends to be widest towards its middle; the apical contour of these tibiae rounded; their outer face of rather uniform surface and in the New World forms approximating the flat, with the apical part as undepressed as the basal; their inner face unevenly gabled, the backward sloping and longer plane terminated only at approximately the posterior contour of the joint, with only a hair-fine posterior rim showing. No tibial comb at the apex of the hind tibiae anteriorly. The hind metatarsi somewhat tapering downward, wider at the base than at the apex but even at the base narrower by a third than are the hind tibiae. The hairs simple and, even when abundant, short and relatively inconspicuous, tending to be longest along the

posterior lateral contour of the hind tibiae. Claws simple, with a well-developed pulvillus.

WINGS: With the first discoidal cell about four-fifths as long as the marginal cell. The transverse cubital veins as a rule only feebly indicated to absent in *limão*, but the first transverse cubital, at least, more distinct in the rare *ehrharti*. The number of hamuli per lower wing usually five, more rarely six, very rarely four or seven.

ABDOMEN: Usually well extended, little telescoped (but more so in *ehrharti* than in *limão*), its width towards the base comparable to the width of the thorax. The chitin for the most part smooth but with traces of punctation where the hairs, which are of variable length and distribution, emerge.

QUEEN

Known only from one species, *limão* (see description of queen of that species). If the queen of *limão* (fig. 4) is representative for the genus, the differences between queen and worker in the structure of the head and of the hind tibiae are less marked than in most Meliponidae.

MALE

DIAGNOSTIC CHARACTERS: Especially differentiated by the following combination of characters: The clypeus very short, less than half as long as it is wide. The labrum with a somewhat tubercular thickening at each lateral extremity. The malar space distinct even if short. The fourth antennal joint (third joint of the flagellum) viewed from below only a little longer than the third; viewed from above barely shorter than the third. The anterior lateral contour of the hind tibiae distinctly convex.

HEAD (FIGS. 5A AND 8A): In the New World species wider than long but not extending to each side quite so far as the outer rims of the tegulae, and smaller than in the conspecific worker. The facial quadrangle relatively wide, the distance between the eyes at a level just below the anterior ocellus only a little less than the distance from the middle ocellus to the apex of the clypeus. The eyes very slightly convergent below, almost parallel sided, and only a trifle wider than the eyes of the conspecific worker. The

genal area much narrower than that of the conspecific worker, hardly as wide as the eye. The clypeus short, but compared to its width relatively longer than is the case in the conspecific worker; its lateral contours very briefly subparallel to slightly divergent at the base, then sharply divergent to the apex, which is approximately truncate throughout and forms an acute angle with the sides of the clypeus; the middle region of the face of the clypeus depressed over at least the apical half. The mandibles, when retracted, overlapping each other, their base about three times as wide as their apex, which has a denticle (sometimes nearly obliterated) at the inner extremity. The malar space much shorter than in the worker, but the rim of the eye nevertheless clearly separated from the base of the mandible. The labrum depressed in the middle and with a tubercle-like eminence (sometimes feeble) at each side. The supraclypeus triangular in contour, longer than wide, its lower part prominent but its upper part recessive, its carinated or carina-like summit connected with the middle ocellus by a rather distinct fossa. The middle ocellus barely anterior to the lateral ocelli, somewhat depressed. The lateral ocelli very slightly tilted, each towards the nearest compound eye; the distance between these ocelli barely greater than that which separates each from the nearest compound eye. A blunt low swelling behind the ocelli and co-extensive with them. The lateral ocelli separated from the posterior edge of the vertex by their own diameter or a little more. The head either almost completely devoid of hair or, if hairs be present, then those hairs for the most part rather short if dense (longer and denser than in the worker). Head either devoid of sculpturing or very finely tessellated over most of its area. The third joint of the antennae (second of flagellum) relatively long; when viewed from above, it is a trifle longer than the next succeeding joint.

THORAX: Either devoid of sculpturing or very finely tessellated over most of its surface, approximating the smooth. The mesonotum, measured at its widest near the base, almost as wide as the combined mesonotum and scutellum are long. The scutellum rounded along its posterior contour and entire (not emarginate) and barely or not at all

impinging upon the hairless dorsal or middle region of the propodeum, which is shiny. The dorsal region of the propodeum, viewed from above, a little shorter than the scutellum. The thorax either without hairs that are readily noted, these being confined to the scutellum and the under side of the thorax, or rather densely hairy over all areas except the dorsal and middle region of the propodeum.

LEGS: Progressively longer from fore pair to hind pair, the hind pair shorter than the combined length of the head, thorax, and abdomen. The tibiae of the fore legs distinctly shorter than their femora; those of the middle legs a little shorter than their femora; those of the hind legs a little longer than their femora but not so long as their femora plus their trochanters. The hind tibiae (figs. 5B and 8B) somewhat elongate oval in outline, the anterior lateral contour more convex, if anything, than the posterior lateral contour, the joint being widest towards the middle; the apical contour of these tibiae more or less rounded; their outer face of rather even surface, approximating the flat; their inner face unevenly gabled, the backward sloping and longer plane terminated only at the posterior contour of the joint. The hind metatarsi very narrow, at their widest only about one-third the maximum width of the hind tibiae, widest near the base, tapering somewhat towards the apex. The hairs abundant though short in *ehrharti*, and sparse (except for the conspicuous hairs on the hind tibiae) in *limão*. Tarsal claws cleft, with a well-developed pulvillus.

WINGS: With the first discoidal cell about four-fifths as long as the marginal cell. The transverse cubital veins as a rule only feebly indicated to absent in *limão*, but the first transverse cubital, at least, more distinct in *ehrharti*. The number of hamuli per lower wing usually from five to six.

ABDOMEN: Well extended, its width towards the base as a rule fully that of the thorax. The chitin for the most part smooth but with feeble isolated small punctures traceable here and there. The hairs sparse dorsally in *limão*, abundant in *ehrharti*.

DISCUSSION

Friese (1903, p. 361) originally erected *Lestrimelitta* as a subgenus of *Trigona* but

subsequently (1912b, p. 169) raised it to generic rank when he described the African *cubiceps*. I am inclined to accept this later judgment. The structure of the head in *Lestrimelitta* is highly individualized and the aberrant relationship of joint 3 of the antennae to the two succeeding joints is also worthy of emphasis. On the whole the relationship of the antennal joints in the Meliponidae is fairly stabilized, although occasionally a species like *Trigona (Hypotrigona) longicornis* Friese asserts its independence. This species, it may be mentioned in passing, alone among the New World *Trigona*, approximates the species of *Lestrimelitta* in the pronounced development of the tubercles on the labrum, although the condition is faintly adumbrated in some other forms.

More exceptional, however, than the structure of the head of *Lestrimelitta* is that of the hind leg of the worker, which is almost disconcertingly different from the other Meliponidae in lacking a comb anteriorly at the apex of the hind tibiae and in being devoid of a depression towards the apical end of the outer face of this joint for pocketing a load of pollen.

How shall we interpret this deficiency of comb and of pollen gathering equipment so at variance with that of other Meliponidae? Friese (1903, p. 361) in erecting *Lestrimelitta* as a subgenus raised the question whether *limão* (the only species of the subgenus then known) might be an inquiline. Later (1912b, p. 169) Friese alluded to the African *Lestrimelitta cubiceps* as a robber bee "which after the manner of *L. limão* Smith of South America attacks in a swarm the industrious species of *Trigona*, drives them away, and takes possession of their supplies of honey. Head- and leg-structure support this conclusion." Subsequently (1931, pp. 3, 6-10) Friese again definitely assigned to *limão* the role of a robber bee as distinguished from an inquiline. The interpretation was based on observations by Ehrhardt, as follows:

"According to the information imparted by Ehrhardt [from São Paulo, Brazil], after the young brood has emerged and the bee community of *limão* has thus been strengthened, scout bees set forth in search of a well developed arboreal nest of some other species of *Trigona* (for instance, *Trigona dorsalis*

[*postica*?], *bipunctata*, *tubiba*) regarding which they gather fundamental information (just as in the case of the honeybee *Apis* a new nesting site is sought for the swarm) in order that thereupon they may, in imitation of ants like *Polyergus*, overwhelm the new *Trigona* nest as a storming party, exterminating the legitimate occupants to the inclusion of their brood and taking possession of the completed combs as well as the available jars, pollen, resin, and wax.

"It is noteworthy that thereupon they immediately enlarge the flight tube and extend it greatly, making provision for innumerable tiny cubbyholes and nooks but with only one of these openings having access to the passageways leading to the conquered nest . . .

"In any event, flight tubes that have been built out extensively and that have an irregularly knob-like surface indicate in the case of *Trigona* nests an attack by robber bees."

Many years before this conclusion regarding the predatory role of *limão* was arrived at by Friese, another investigator (F. Müller, 1874b, p. 103) had voiced a similar view. Of *limão* Müller stated that it "never appears to collect honey or pollen from flowers, on which, at least, I have never seen it. It robs other species of their provisions and sometimes takes possession of their nests, killing or expelling the owners. The hives in my garden have often been invaded, and two of them destroyed, by these robbers, and I have seen in the forest several nests, formerly inhabited by other species, occupied by them."

To these observations I am privileged to add also those of C. D. Michener, who on 10 different occasions in Panama observed *limão* attacking colonies of *Trigona* (*Nannotrigona*) *testaceicornis* variety *perilampoides* Cresson and only this species. While the booty-minded individuals of *limão* did not actually take permanent possession of the homestead of the victimized bees, they nevertheless nibbled at the waxen building materials, acting as a kind of demolition squad by reducing and fraying the entrance tube. Meantime the pollen-laden foragers of *perilampoides* returning from the field flew futilely in front of their ravished home, kept at

a distance by the aggressive attitude of the *limão* workers guarding the entrance (Michener, 1946, pp. 196-197).

The statements of F. Müller, of Friese, and of Michener would seem to be conclusive as to the propensities of *limão*, and yet, like Rau (1933, pp. 32-34), I find it hard to believe that these bees are completely predatory. The nest of *limão* on Barro Colorado Island, Canal Zone (pl. 3, fig. 3), to which Rau refers has been on the same site for years. I first had a view of the nest in the fall of 1930, but it was still functioning when I revisited Barro Colorado in 1933, and the colony seemed as prosperous and active then as it was at the time of my first visit. I do not know how long prior to 1930 the *limão* bees may have been in occupation of the site but, even if one takes 1930 as the starting point, it is difficult to believe that the "robbers" could have lived on the stored loot for so extensive a period without replenishing the supply through their own efforts. While fully accepting the observations of those who have witnessed the assaults on colonies of other bees by *limão* and the occupation permanently of these colonies by the invader, it seems legitimate to conclude that this puzzling species is at least not dependent on assault and robbery for its existence, although, due to its deficient collecting equipment, it may find these violent methods the easier course. In its reactions to man at any rate, it is usually non-aggressive, and more than one observer has commented upon its mild behavior.

Nor is the nest on Barro Colorado Island the only one that would seem to absolve *limão* from the imputation of maintaining its existence solely by assault and theft. An interesting case is supplied by H. von Ihering (1903, p. 261), who, although he referred to *limão* as a robber bee, stated in the next breath that at one time he kept alive a nest of this species in Rio Grande do Sul, Brasil. "There was no forest near the dwelling and for this reason, if for no other, the bee was obliged to work. I cannot, therefore, agree with the opinion of Fritz Müller according to which these robber bees do not work self-supportingly but exist only by robbery." Moreover, Fiebrig (1908, pp. 374-386), who transferred a colony of *limão* to a large glass

cylinder, found that the bees not only made structural additions to the nest in this new site, but when opportunity was given them to fly forth, they returned pollen laden.

Another bit of evidence that may have bearing on the alleged predatory habits of *limão* is the circumstance that most writers who have commented on the quality of the honey indicate that in many cases at least it is poisonous. This, according to Holmberg (1887, p. 261), Ambrosetti (1895, p. 699), and Silvestri (1902b, pp. 127-128), was the reputation it had in Misiones, Argentina, where it was said to cause fever, upset stomach, and other unpleasant symptoms, even paralysis, although in Matto Grosso, Brazil, according to Silvestri, it was consumed without producing such injurious consequences. Similarly Bertoni (1911, p. 141), writing of the bees of Paraguay, indicated that at times the honey obtained from nests of *limão* caused intestinal disturbances if eaten in quantity, although this was far from being invariably the case. According to the account in the paper by H. von Ihering (1903, pp. 271-272) the only bee in Rio Grande do Sul, Brazil, that was said to have poisonous honey was *limão*, and von Ihering reasons, with much plausibility I think, that it is *limão* that is referred to in the communication addressed by Padre José de Anchieta, under date of May 31, 1560, from São Vicente (now São Paulo, Brazil) near Santos to the Jesuit General. In that communication, according to H. von Ihering, the padre commented as follows: "Of the many species of honey I shall lay stress only on one, which the natives call Eira-Aquaíetá,¹ meaning a bee nest with many entrances to the hive. As soon as one tastes of this honey, one feels it in all one's limbs; there result pains, chills, and cramps, vomiting and nausea." H. von Ihering expressed "little doubt that the reference is to *Trigona limão* F. Smith, the large flight tube of which is provided with numerous little pipe-shaped protuberances some of which are closed and others of which are open." Also because of the description of the flight tube, von Ihering believed that the references to injurious honey contained in a

book by von Martius (1867, pp. 52 and 454) bespeak the activities of *limão*.

Now, while instances of poisonous honey are cited in the case of other stingless bees as well as some of the social wasps, I cannot help thinking that the rather persistent association of poisonous honey with *limão* gives this species preëminence in evil repute. But if *limão* lives by robbery, or primarily by robbery, how can one account for the fact that in such a disproportionate number of cases it selects for its attack nests that contain supplies of toxic quality? Far more likely, it seems to me, is the assumption that *limão* in the main does its own provisioning and that the poisonous nature of its honey noted in so many cases is due either to some secretion added by the bee before regurgitating the nectar it gathers or, more likely, to a partiality in its floral visits for species of plants that are poisonous. In this connection it may be noted that the wasp *Nectarina lecheguana* sometimes produces honey that is poisonous and that in its case a similar explanation has been offered to account for the noxious product (L. Digue). On the other hand, no one has observed *limão* visiting flowers and that very fact encourages the belief that *limão* gets its supplies elsewhere.

Before closing this controversial question regarding the status of *limão* in its relationship with other species of the bee community, let us turn to a field observation which W. Weyrauch has sent me. His notation, which applies to specimens (his No. 151) of *limão* collected at San Ramon, Valle de Chanchamayo, Peru, reads as follows: "Driven out of their nest in a wall by a swarm of *jaty* after a battle lasting for two days." Here indeed is what on first impression seems an astounding situation. The little *Trigona* (*Tetragona*) *jaty* F. Smith, one of the smallest of the stingless bees and one structurally not well fitted seemingly by nature to defend itself, is here depicted as actually attacking, and attacking successfully, one of the putative villains of the bee world in its very citadel and driving that villain out of the stronghold.

My first reaction was one of incredulity. It was as though the lamb had been reported devouring the wolf. I was reluctant to question the interpretation of so excellent an observer as Weyrauch, but I could not help

¹ This bee is referred to elsewhere by Anchieta (1812, p. 155) as "eira quáyeta."

wondering whether he might not have been confused as to the original occupant of the nest and that, perhaps coming upon the two struggling species in the midst of their battle, he had concluded that *jaty* was the aggressor because that species finally remained in possession of the nest. The following citation from Marianno did not entirely clarify the situation but at least gave plausibility to Weyrauch's interpretation. Marianno (1911, p. 112) said of *jaty* that "it defends itself valiantly against other species and battles with the large *Melipona*." Both defense and aggression are suggested by this statement, and I was left wondering whether *jaty* was indeed, as Weyrauch concluded, the dispossessor on this occasion and *limão* the victim of aggression, or whether *limão* was acting up to its reputed character without achieving the loot.

Further search of the literature, however, completely dispelled my doubts as to the correctness of Weyrauch's conclusion. Substantiation for Weyrauch's interpretation is found in Bertoni (1911, pp. 139, 143), who in commenting on the combativeness of stingless bees in general pronounced the midget *jaty* the most successful warrior of them all. The observation made by Weyrauch points to the fact that *limão* is at least not always successful in its struggle for mastery and confirms the doubt whether it is exclusively devoted to a career of rapine without at least intervals of honest foraging. If, after two days of combat with *jaty*, *limão* gave up the fight and retreated, then it would seem unlikely that robbery is the sole source of its livelihood.

The honey of *jaty* is usually among the most delicious and wholesome produced by stingless bees. The honey of *limão* has in general a rather evil reputation. If robbery were habitual with either of these species, it would seem unlikely that the quality of their respective honeys—one good, the other bad—would be so constant.

While *limão* is the species against which the most persistent accusations of robbery are leveled, and it has even been observed robbing the hive of the honeybee (Ballou, 1945, p. 129), it does not bear alone the opprobrium of engaging in anti-social activities. Salt (1929, p. 461) in his industrious search

through the literature has assembled instances of combats between different species of stingless bees. An early case is that of which Drory told (1873a, p. xxxii) concerning a species in Bahia with the popular name of "tiuba amarella" [*Trigona* (*Scaptotrigona*) *postica* Latreille]. This bee, according to information that Drory received from Brunet, a resident in Bahia, defends itself against its enemies and battles successfully against wasps two or three times its own size. In a single nest of "tiuba amarella" more than 30 wasps were found dead. A little later Girard (1875a, p. 572) summarized various combats he had observed between *Melipona fasciata* variety *scutellaris* Latreille and *Melipona marginata* Lepeletier, between what was probably *Trigona* (*Scaptotrigona*) *postica* Latreille (misinterpreted as "*dorsalis*" F. Smith) and *Trigona* (*Oxytrigona*) *tataira* variety *flaveola* Friese, and between *Trigona* (*Scaptotrigona*) *postica* Latreille and *Trigona* (*Tetragona*) *angustula* Latreille. He even recorded an encounter between the species last mentioned and the honeybee, *Apis mellifera*.

It is of interest that "*dorsalis*," which is mentioned doubtfully by Girard¹ as a combatant, is spoken of in no uncertain terms by H. von Ihering as a very aggressive bee (1903, p. 261). Indeed it is von Ihering's conclusion, based on field observations, that this bee (in all probability *postica* or close to it) is wont not merely to rob its neighbors but to drive them out of their nests and itself to take possession of the vacated homestead. Thus H. von Ihering reported:

¹ Although Lutz and Cockerell (1920, p. 497) indicated their belief that Girard's interpretation (1874b, p. cvi) of *dorsalis* is the same as that of F. Smith in his original description (1854, p. 411), I am of the opinion that this is not the case. In another allusion to *dorsalis* Girard (1875a, p. 572) indicated his doubt whether a stingless bee of the species that had attacked *Trigona flaveola* was *postica* or *dorsalis*. The very fact that Girard could not decide to which form, *postica* or *dorsalis*, to assign the specimens would seem to prove that in Girard's conception these two forms were very closely connected. The true *dorsalis* is, however, a member of the subgenus *Tetragona* while *postica* is placed in the subgenus *Scaptotrigona*. The two bees are different from each other in nearly every respect, and no one would be inclined to associate them unless he placed upon the one or the other an interpretation different from that here arrived at. Similarly it is doubtful whether H. von Ihering's *dorsalis* (1903, p. 211) is correctly associated with F. Smith's bee of that name.

"It has happened several times that I have lost nests which I had contemplated acquiring through their prior occupation by a swarm of *Trigona dorsalis*. In one such case I saved the flight-hole as well as the entrance tube. . . . The wide funnel of wax characteristic of the robber bees is in this case superimposed on the entrance, which had been constructed of mud by *Melipona anthidioides* [the evicted occupant].

"After years of painstaking effort I succeeded in locating a nest of *Trigona cagafogo*, feared on account of its painful bite, but when at last the nest was to be called for, it had been destroyed by a swarm of *Trigona dorsalis*, which had made its nest in the hive. The seizure of the nest is achieved after intense combat, in which the bees offering resistance are killed. In these struggles *Trigona dorsalis* comes out the victor if for no other reason than that its somewhat more powerful mandibles assure it a certain superiority over its opponents. Only the dwelling is utilized by the robbers; the brood combs and the provision containers are destroyed and removed, being replaced by others newly constructed."

But while H. von Ihering rated this bee as no less predaceous than *limão*, in neither case did he draw the conclusion that robbery was the sole mode of livelihood. His remarks (1903, p. 259), which apply not only to these species but to the Meliponidae as a whole, are worthy of repetition:

"There are among the Meliponidae robber bees in all gradations. An inclination to rob is probably present in all social bees, even in the case of *Apis mellifica* swarms are not infrequently observed which plunder other hives. Such occasional robberies occur probably among all the Meliponidae, but can readily be distinguished from the thieving habits of certain species of *Trigona*, which, compared with the occasional pilferers, stand forth as thieves by profession and robbers by vocation. Even the worst among them are, however, still worker bees, and as soon as occasion requires, turn to the gathering of honey and pollen.

"There is an aphorism to the effect that 'opportunity makes thieves,' and this explains why even the harmless species of *Melipona* do not scruple to steal from neighboring hives. Everywhere, where industry

creates values and where there is property, there occur as natural concomitants theft and robbery. This applies to the animal world as well as to the human. There is an inclination, easily understandable on psychological grounds, to attain without effort what others have gathered through hard, prolonged labor. Among the various hives of *Melipona* which I kept in a living condition at only slight distances from one another these thefts could be noted regularly, and were as numerous when the hive plundered was of the same species as when a different species was made the victim."

The nest interior of *limão* as described by Silvestri (1902b, pp. 127-128) consists of superimposed horizontal combs enclosed by an involucre and of moderately large oval provision containers. It is the external architecture of the nest, however, that is the more deserving of emphasis. The flight tube is impressively long and large. H. von Ihering (1903, p. 223) recorded one that had a length of 16 cm., and another that stretched out from the nest for a distance of 19 cm.; Rau (1933, p. 32) estimated the length of the tube he observed as 10 inches, while Bertoni (1911, p. 141) records one extending outward for the impressive length of 35 cm., the maximum length represented among those he noted. The last-mentioned tube at its widest was 12 cm. The irregularly knob-like surface of the tube, to which Friese on the authority of Ehrhardt refers in a passage already quoted, doubtless resembles the condition of the tube I saw on Barro Colorado Island, Canal Zone, which was irregular and rough with many stalactite-like extensions, particularly on the under side. Rau (1933, p. 32) has figured this tube or perhaps one of later construction (though leading to the same nest), and it has also been photographed by Shattuck (pl. 3, fig. 3). In the picture by Shattuck the stalactite-like extensions are longer than in the picture by Rau, indicating that slight differences may occur even when the artisans that built the earlier flight tube and those that fashioned its later replacement are successive generations of the same colony. On the whole, however, the two tubes of this nest, constructed at different times, show a rather striking similarity. Not so very different is another flight tube from southern Brazil

(pl. 3, fig. 2), in which, however, the "stalactites" are rather more crowded. Probably these are just individual differences without regional constancy, and they are figured on plate 3 of this paper merely to illustrate the range in building design.

More puzzling is the nest entrance figured by Silvestri (1902b, pl. 3, fig. 43) and here reproduced as plate 3, figure 1. Both Holmberg (1887, pp. 284-285) and Silvestri (1902b, p. 128) referred to the nest entrance of *limão* as composed of a spongy plate or mass with, according to Silvestri, five or six tubes of variable length. It is not clear whether the nest Silvestri figured came from Santa Ana, Misiones, Argentina, or from Coxipò, Matto Grosso, Brazil, but the likelihood is Santa Ana. Thus it is possible that towards the southern extreme of its range *limão* builds differently from what it does farther north.

According to Bertoni (1911, p. 141) the Guaríní name for *limão*, which is "eirati," is descriptive of the nest entrance. "Ati," the concluding element of the popular name, means horn and refers to the appendix-like formations on the entrance.

When, according to Bosetti (cited by Holmberg, 1887, pp. 284-285), the mass constituting the nest portal has attained a certain size, it breaks off and falls to earth. The bees thereupon form a new entrance, which in its turn also drops down through its weight in the course of time. Thus heaps of such portals are formed, which are characteristic of this species and sometimes yield as much as 50 pounds of wax.

Hermann von Ihering (1903, p. 223) noted that the nest of *limão* is apt to be located in hollow tree trunks, usually at a considerable height. But the nest on Barro Colorado Island, Canal Zone, is only about 1 foot from the ground, and the nest of the colony that Fiebrig (1908, p. 385) domesticated was originally in a tree hollow about 1 meter above the ground. One of the nests noted by Silvestri (1902b, p. 127) was located in a wall, and Alfaro wrote me regarding a nest he observed at San Isidro, Costa Rica, which was located in the wall of a wooden house and had a spout 8 inches long (pl. 3, fig. 4).

We have seen that stingless bees are on occasion victims of mass attacks by their own relatives. Other invertebrate enemies are ants

and wasps as well as cockroaches. The protective measures against intruders vary somewhat from species to species. The structure of the nest is in itself well designed to wall out those who have no proper place in the economy of the colony. The approach to the interior is through the flight hole, and this is in some species so small that a single guarding bee can close the orifice with its head. At night, or under certain conditions also by day, such a hole may be sealed up with wax and thus made safe against the prowler or dispoiler.

Other species, with large flight tubes, have during the daytime at least a goodly number of defenders on guard, studding the inner wall of the tube so thickly that the would-be aggressor attempts an entrance only at her peril. I have seen such an array of defenders martialed in the tube of *limão*, but it is not the sole defensive measure on which this bee relies. According to Fiebrig (1908, pp. 375, 380), *limão*, as do some other Meliponidae (Fiebrig mentioned especially *Trigona mosquito* variety *emerina*), protects the approaches to its nest by laying down numerous little globules of wax, for the most part no bigger than a pin head, that function as a sort of tanglefoot to intruding ants. But notwithstanding these precautions Fiebrig's colony of *limão*, which had been transferred from its natural site to a large glass cylinder, succumbed to the ravages of ants. Fiebrig was inclined to think that the success of the ants was ascribable to the artificial conditions under which the *limão* nest was established, not to a natural disparity between bee and ant in combat strength or resourceful device.

Towards man *limão* behaves tolerantly. H. Müller (1875b, p. 43), citing the experiences of his brother, F. Müller, with this bee, stated that members of a colony would retreat as though in fear if one knocked on the tree or box in which the colony was housed. The nest previously alluded to on Barro Colorado Island, Canal Zone, could be approached with impunity.

KEY TO THE SPECIES OF *Lestrimelitta*

WORKERS

1. The head almost wholly black, with no side-facial maculations and with as a rule at most the apex of the clypeus, labrum, mandibles,

scape in front, and flagellum beneath more or less ferruginous, and even some or all of these parts sometimes suffused with black. The head, thorax, and in more varying degree the abdomen largely devoid of erect or semi-erect hairs, with resulting shininess. Chitin smooth *limão* F. Smith

A large, ivory-colored maculation on each side of the clypeus, and the clypeus itself ivory colored to ferruginous. Especially the thorax and abdomen (the latter on at least the apical half of all its tergites) rather densely covered with erect to semi-erect hairs. At least the thorax with rather dense, if fine, tessellation *ehrharti* Friese

QUEENS

Only the queen of *limão* is known.

MALES

1. The maculations on the lower half of the face ferruginous to sometimes yellow, the maculation on the clypeus confined to the apical part. The head, thorax (except scutellum), and abdomen (except its apico-lateral contours) devoid or largely devoid of erect hairs, shiny. Sternite 6 emarginate at the middle *limão* F. Smith
- The lower half of the face with cream-colored maculations, the side-facial maculations extending upward halfway to the level of the ocelli. The head, thorax, and abdomen rather conspicuously hirsute. Sternite 6 with a strong median spine. *ehrharti* Friese

Lestrimelitta limão (F. Smith)

"Efra quāyetā," DE ANCHIETA, 1560 (1812, p. 155).

Trigona limão F. SMITH, 1863a, p. 506.

"Iratí," "Iriti," "Irutim," VON MARTIUS, 1867, pp. 52, 454.

Trigona limão, F. MÜLLER, 1874b, p. 103.

"Limão," ANONYMOUS, 1878b, p. 74.

Trigona limao, H. VON IHERING, 1886, p. 184.

"Eirā-ti" or "Irā-tinga," HOLMBERG, 1887, pp. 260-261, 266, 284-285, 287.

Melipona limao, PECKOLT, 1893, p. 580.

Melipona limao, PECKOLT, 1894, p. 234.

"Iratí" or "Coalatí," AMBROSETTI, 1895, p. 699.

Melipona limao, DALLA TORRE, 1896, p. 580.

Trigona limao, "Eirā-ti," "Arancín," SILVESTRI, 1902b, pp. 126-128, fig. 1, pl. 1, figs. 7-9, pl. 3, fig. 43.

Trigona (Lestrimelitta) limao, FRIESE, 1903, p. 361.

Trigona (Lestrimelitta) limao variety *rufipes* FRIESE, 1903, p. 361.

Trigona (Lestrimelitta) limao variety *rufa* FRIESE, 1903, p. 361.

Trigona limao, H. VON IHERING, 1903, pp. 223, 239, 240, 261, 271-272, 278, pl. 17, fig. 3, pls. 18, 19.

Trigona limeo, GRÜNBERG, 1904, p. 17.

Trigona limão, H. VON IHERING, 1904b, pp. 379, 382, 384.

Melipona limao, RUDOW, 1907, p. 30.

Lestrimelitta limão, FIEBRIG, 1908, pp. 374-386.

Trigona limão, DUCKE, 1908b, p. 81.

Trigona limão, MARIANNO, 1910c, p. 10.

Trigona limao, BERTONI, 1911, p. 99 (identification by H. Friese).

Lestrimelitta limao, BERTONI, 1911, p. 141.

Trigona (Lestrimelitta) limão, MARIANNO, 1911, pp. 8, 24, 139-140, pl. 2.

Melipona limão, RUDOW, 1914, p. 249, fig. 13.

Melipona limão, DUCKE, 1916, p. 13, opposite p. 28, p. 29, pl. 4, fig. 10.

Trigona limao, WHEELER, 1923, fig. 47D.

Lestrimelitta limao, LUTZ, 1924a, pp. 205, 207, 208, 211, 212, 215, 216, 220, 221, 226, 231, 232.

Melipona limao, DUCKE, 1925, pp. 342, 348, 363-365, text fig. E, pl. 3, fig. 3.

Trigona (Lestrimelitta) limao, WHEELER, 1926, p. 342.

Trigona (Lestrimelitta) limao, WHEELER, 1928, p. 277.

Trigona limao, SALT, 1929, pp. 461-462.

Melipona limao, ALFKEN, 1930b, p. 8.

Lestrimelitta limao, FRIESE, 1931, pp. 3, 4, 5, 6-12, 13, 14, figs. 1-4.

Melipona limão, GUENTHER, 1931, pp. 297, 298, 376.

Trigona limao, SCHWARZ, 1932a, p. 253.

Lestrimelitta limao, RAU, 1933, pp. 32-34 (identification by H. F. Schwarz).

Lestrimelitta limão, SCHWARZ, 1934, pp. 2, 23.

Lestrimelitta limao, MAIDL, 1934, pp. 316-317, 318-319, 573, 575, 576, 580, 584.

Lestrimelitta limao, SAPPER, 1935, p. 184.

Trigona (Lestrimelitta) limão, SCHWARZ, 1938, pp. 441, 451.

Melipona (Trigona) limão, R. VON IHERING, 1940, pp. 404-405, 467, 866.

Lestrimelitta limao, MOURE, 1944a, p. 70.

Lestrimelitta limão, SCHWARZ, 1944, pp. 417, 426.

Lestrimelitta limao, BALLOU, 1945, p. 129.

Lestrimelitta limão, MICHENER, 1946, pp. 196-197 (identified by H. F. Schwarz).

WORKER

DIAGNOSTIC CHARACTERS: Clypeus wholly, or virtually wholly, and sides of face wholly, black. Clypeus very strongly foveate at apical

middle. Head, thorax, and four basal tergites of abdomen largely hairless. Abdomen black to dark brown.

HEAD (FIG. 3A): Smooth, with the structural characters noted for the genus *Lestrimelitta*. The lower half of the clypeus very abruptly declivitous at its middle and strongly and rather triangularly foveate, with a longitudinal incised line traceable in the fovea. Black except for usually some or all of the following parts, which tend to be more or less ferruginous: apex of clypeus, labrum,

are very sparse but in other cases of increasing density, reaching their maximum concentration in specimens from Tena, Ecuador, and in a few specimens without locality designation. The erect hairs of the thorax exceedingly few. At first glance they seem to be confined to the scutellum, where they are in most instances long and black or blackish. As a rule these scutellar hairs are much longer than the usually black or blackish hairs along the basal edge of the mesonotum, but their length is variable and in a few instances,

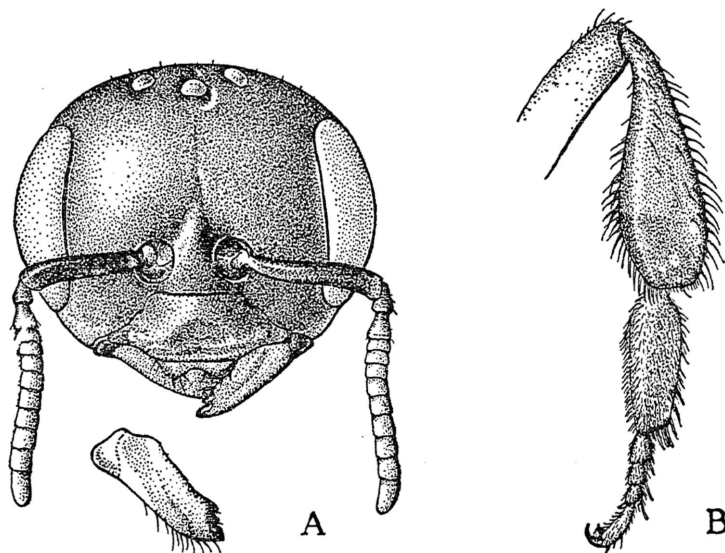


FIG. 3. Worker of *Lestrimelitta limão* (F. Smith). A. Head and mandible. B. Tibia and tarsal joints of hind leg. Based on a specimen from Barro Colorado, Canal Zone. Drawings by Shirley H. Risser.

mandibles, scape in front, and flagellum beneath. Except for a fringe of moderately long, usually silvery gray to ferruginous hairs fringing the lower edge of the mandibles, the evidences of hair, even on the vertex, are so feeble that the head usually passes as hairless or nearly so, and the smooth exposed chitin is correspondingly shiny.

THORAX: Smooth, black, nearly as shiny in many specimens as the head but usually covered (except for the dorsal and middle region of the propodeum) with microscopic and, as a rule, appressed hairs that impart a more or less sericeous sheen especially to the mesonotum. These microscopic hairs are present in varying degree. Sometimes they

especially in specimens from localities in Costa Rica, they are relatively short. To instance a reverse extreme: in the case of specimens from Northwest District, British Guiana, there are no erect hairs anteriorly along the mesonotum with which to compare the scutellar hairs, which in these specimens are rather exceptionally long. The under side of the thorax with more or less erect silvery gray hairs.

LEGS: Variable in coloration, ranging from predominantly reddish or reddish brown to predominantly black or fuscous. In all, or nearly all, specimens the trochanters, at least on their under side, and frequently also more or less the femora, as well as the small joints

of the tarsi and not infrequently also the metatarsi, are ferruginous. The femora and tibiae vary most, being predominantly black or blackish in specimens from localities in Guatemala, Trinidad, Tena in Ecuador, San Ramon in Peru, Baurú and Jundiahy in Brazil, and in Paraguay. In some of these darker specimens the apex of the tibiae, more particularly the hind tibiae (fig. 3B), are more or less extensively reddish and the under side of the femora, more particularly of the hind femora, inclines sometimes to red (these tendencies are more or less pronounced in the specimens from Tena, Ecuador, and those from Paraguay, but may be the last vestiges of a callow condition and therefore not representative). Specimens from Northwest District, British Guiana, have reddish brown legs with only faint clouding here and there, but as the specimens are only two in number I hesitate to conclude that this condition is representative, especially as they have certain other earmarks of the callow. A large series from Barro Colorado Island, Canal Zone, represents the reddish brown extreme. In the case of these Canal Zone *limão* all the femora and tibiae tend to be reddish brown, but, by way of contrast, they have some or all of the following black maculations: apex of femora, especially the hind pair, and (usually strongly indicated) a stripe on the under side of the hind femora, apex of outer face of hind tibiae and usually a narrow band as well upward along the posterior contour, base and apex of inner face of hind tibiae with a narrow anteromedian stripe connecting them. It will be noted that in the presence of a black stripe on the under side of the hind femora and in the dark maculation of the apex of the outer face of the hind tibiae these specimens reverse the condition of such specimens as those from Tena, Ecuador, and from Paraguay. The maculation of the inner face of the hind tibiae of the Barro Colorado specimens is approximated in specimens from Costa Rica, more particularly those collected at San Isidro, and the coloration of the outer face of this joint approximates not only in the Costa Rican specimens but also, if obscurely, in some of the South American specimens the condition represented more emphatically in the Barro Colorado Island examples. The hairs of the legs on the whole sparse, short,

and inconspicuous. Those on the coxae and trochanters beneath short and silvery gray; those on the femora likewise silvery gray but very inconspicuous, for the most part microscopic and appressed, perhaps densest and most readily traced on the outer or anterior face of the hind femora. The outer face of the fore and middle tibiae with for the most part only microscopic appressed hairs that have a sericeous sheen; especially the middle tibiae, in addition, with at least a few dark erect hairs towards their posterior lateral contour. The outer face of the hind tibiae devoid, or virtually devoid, of hairs of any kind and correspondingly shiny, its anterior and posterior lateral contours, however, fringed rather densely with simple hairs, those along the posterior lateral contour black and as a rule distinctly longer than those along the anterior lateral contour. The inner face of the hind tibiae rather densely covered with microscopic silvery gray hairs. The hairs on the metatarsi inconspicuous, for the most part appressed, such erect hairs as there are being usually concentrated towards the posterior lateral contour of the joint. Metatarsal brushes pale golden or even silvery.

WINGS: Hyaline to subhyaline, with brownish to fuscous venation and stigma, and more or less concolorous tegulae. The transverse cubital veins only very feebly indicated to absent. The number of hamuli per lower wing ranges from four to seven, with the prevalent number five or six. Of 148 wings examined, 113 had five hamuli, 32 had six hamuli, two had four hamuli, and one had seven hamuli, making an average of 5.22. The preponderance of specimens with five hamuli was particularly marked in the series from Barro Colorado Island. Certain other localities, notably those of Costa Rica and Peru, showed a preponderance of specimens having six hamuli instead of five and, if the representation from these localities had been as large as that from Barro Colorado Island, very likely the average would have far exceeded 5.22.

ABDOMEN: Brownish black to black, smooth and shiny, but with usually a few scattered shallow punctures here and there over the apical half of tergites 2 to 6. The hairs of the tergites black, inconspicuous, for the most part appressed, and short, barely

traceable and scant on the basal tergites but denser and longer on tergites 5 and 6 or, in some cases, tergites 4 to 6. The sternites with usually a few erect or semi-erect grayish to blackish hairs at the middle of the apex of each, and on each side of these tufts there is on sternites 3 to 6 a sericeous silvery gray patch of appressed hairs.

the tegulae to the outer rim of the other. The facial quadrangle wide, the distance between the eyes at a level just below the anterior ocellus about equal to the distance from the middle ocellus to the apex of the clypeus. The eyes parallel sided to barely convergent above, relatively short (barely shorter than is the eye of the worker from the same nest) and

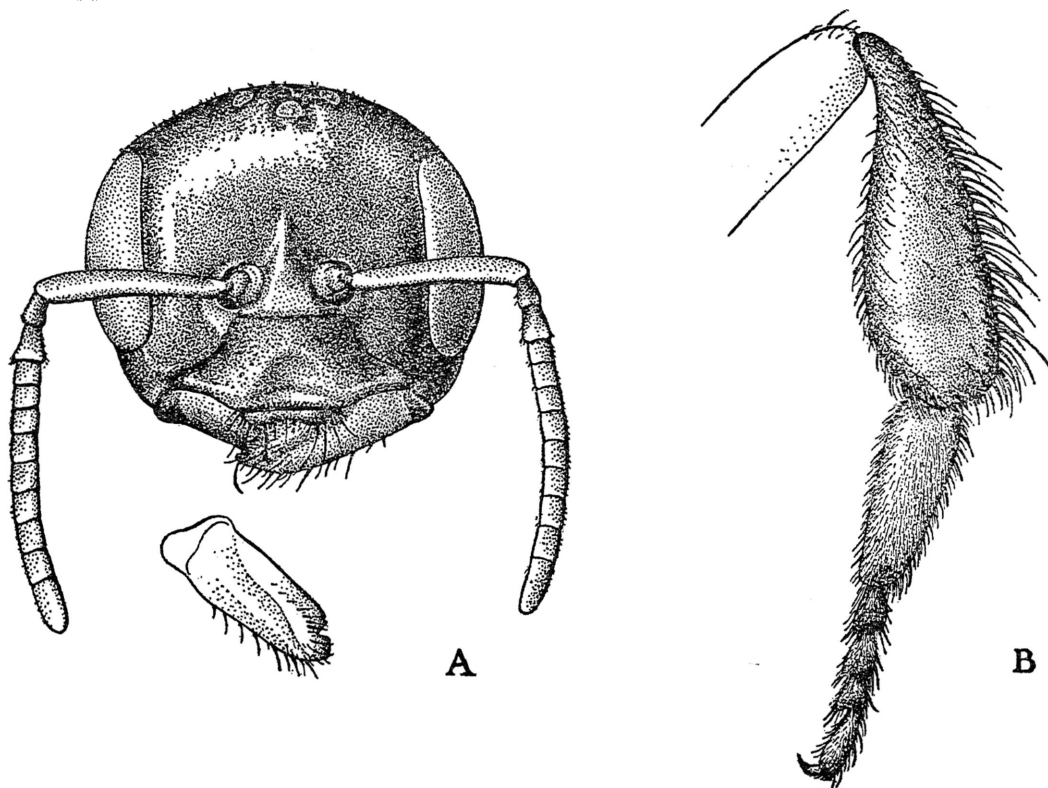


FIG. 4. Queen of *Lestrimelitta limão* (F. Smith). A. Head and mandible. B. Tibia and tarsal joints of hind leg. Based on a specimen from Rio Acre, Brazil. Drawings by Shirley H. Risser.

MEASUREMENTS: Length about 5.5 to 6.25 mm.; width of thorax about 2 mm.; length of forewing, including tegula, 5 to 5.5 mm.

QUEEN¹

HEAD (FIG. 4A): Devoid of sculpturing, somewhat narrower than the maximum width of the mesonotum and very notably narrower than the distance from the outer rim of one of

narrow (notably narrower than the wide genal area). The clypeus about three times as wide at its widest as it is long; its sides subparallel to slightly divergent over their basal half, much more sharply divergent over their apical half; the apico-lateral extremities forming a strongly acute angle with the apical contour of the clypeus, this apical contour being almost truncate with a rather feeble recession towards each of its extremities. The clypeus raised somewhat above the level of the sides of the face, its lower half or a little more than its lower half strongly and rather triangularly foveate, with a longitudinal incised line traceable in the fovea. The man-

¹ Based on five specimens, three gravid, two virgin. There was a gravid specimen from each of the following localities: Rio Acre, Acre, Brazil (the largest specimen); Paraguay; San Rafael, Trinidad, British West Indies. From the last-mentioned locality were obtained the two virgin queens.

dibles overlapping, wider (but not much wider) at the base than at the apex, approximately the outer two-thirds of their apical edge edentate, the inner one-third with two very tiny denticles that are sometimes indistinct and blurred. The malar space well developed, at its shortest (towards the inner extremity of the base of the mandible) about twice as long as the flagellum is wide. The labrum with a rather noticeable tubercle towards each lateral extremity. The supra-clypeus a little more prominent than the clypeus, subtriangular in contour, a little longer than wide, its somewhat carinated summit pointing towards the middle ocellus. The middle ocellus slightly anterior to the lateral ocelli. The distance between the lateral ocelli distinctly less than that which separates each lateral ocellus from the nearest compound eye towards which it is feebly tilted. The region behind the ocelli slightly swollen. The small lateral ocelli distant by several times their own diameter from the edge of the vertex. The head black to deep reddish black, with the mandibles (except for usually the black basal prominences and apical edge), the labrum, the apical edge of the clypeus, the antennal sockets, and the flagellum beneath red (but in the largest of the specimens, that from Rio Acre, red invades even the upper part of the head). The chitin almost completely bare and shiny except for a few long pale to stramineous hairs tufting the tubercles of the labrum and somewhat similar hairs fringing the mandibles below. The vertex glabrous or virtually so.

THORAX: Devoid of sculpturing and wide, distinctly wider at the base of the mesonotum than the combined length of the mesonotum and scutellum. The posterior contour of the scutellum rounded, not in the least over-roofing the hairless and shiny dorsal or middle regions of the propodeum. The scutellum a little longer than the dorsal region of the propodeum when viewed from above. The mesonotum and in the main also the scutellum black but the sides of the thorax and the propodeum more or less reddish brown. The mesonotum, as well as the sides of the thorax, covered fairly densely with exceedingly minute pale hairs that give a sericeous sheen to these parts. The sides of the propodeum with no, or virtually no, such hairs, and

nearly or just as shiny as the dorsal and middle regions of the propodeum. The silvery gray hairs on the scutellum, particularly the posterior part of the scutellum, are, as in the worker and the male, the most conspicuous of the thoracic hairs.

LEGS: Longer and more robust than those of the worker or the male, progressively longer from the fore pair to the hind pair, the hind pair somewhat comparable in length with the head, thorax, and abdomen combined of the non-physogastric queen. The tibiae of the fore and middle legs distinctly shorter than their respective femora, those of the hind leg longer than their femora but distinctly shorter than their femora plus their trochanters. The hind tibiae (fig. 4B) very similar in shape to those of the worker and the male, rather elongate oval in outline, their anterior lateral contour a little more convex than their posterior lateral contour, the joint being widest towards the middle; their apical contour more or less rounded; their outer face of rather even surface, departing but little from the flat, even anteriorly; their inner face unevenly gabled, the backward-sloping and longer plane terminated almost at the posterior contour of the joint, with only a very narrow rim surviving. The hind metatarsi about half as long and half as wide, respectively, as are the hind tibiae; widest at the base, they taper to a narrowed apex. The legs reddish to reddish brown. The hairs long and conspicuous only on the posterior lateral contour of the hind tibiae; those on the several coxae anteriorly, on the trochanters beneath, and on the femora (especially basally beneath) very short and silvery gray. The middle tibiae densely clothed, especially on their outer face, with short yellowish hairs that are far more conspicuous than the very microscopic sparse hairs of the fore tibiae. The outer face of the hind tibiae largely glabrous, but the anterior lateral contour with rather short yellowish to brownish hairs and the posterior lateral contour with much longer hairs of like color; the unequally gabled inner face of the hind tibiae covered densely with microscopic silvery gray hairs. Fine short silvery gray hairs cover the outer face of the metatarsi; the soft metatarsal brushes on the inner face are light golden.

WINGS: Hyaline to subhyaline, with brown-

ish to fuscous venation and stigma, and reddish brown tegulae. The transverse cubital veins feebly indicated to absent. The first discoidal cell about four-fifths as long as the marginal. The number of hamuli per lower wing ranged from four to five with an average of 4.6. There were four wings having five hamuli and three wings having four hamuli. All of the latter were from San Rafael, Trinidad.

shorter and of more limited distribution than those on the tergites: sternite 1 silvery gray tomentose, sternites 2 to 5 with a narrow band of pale hairs that are scant on at least sternites 2 and 3. Sternite 6 strongly emarginate at the apex, resulting in twin, lobe-like formations that are covered with silvery gray sericeous hairs and fringed with long hairs.

MEASUREMENTS: Length 9 to 10.5 mm. (gravid specimens), 7 mm. (virgin specimens);

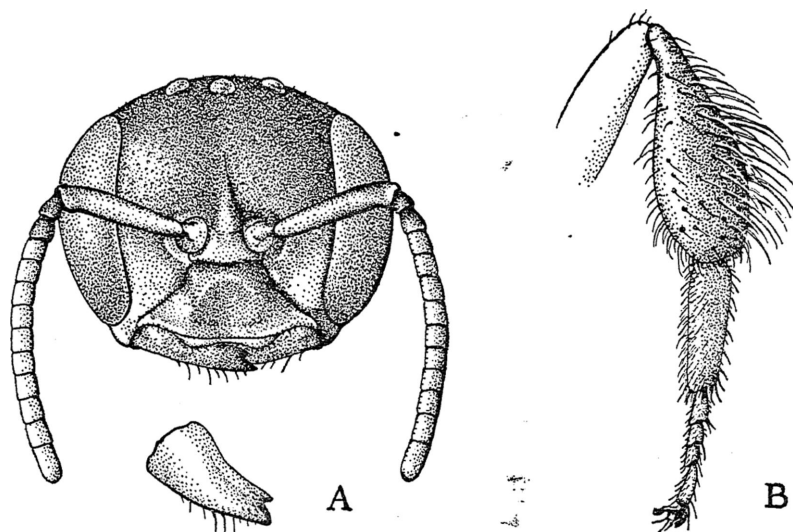


FIG. 5. Male of *Lestrimelitta limão* (F. Smith). A. Head and mandible. B. Tibia and tarsal joints of hind leg. Based on a specimen from Baurú, Brazil. Drawings by Shirley H. Risser.

ABDOMEN: Greatly distended in the gravid specimens, not only wider but of greater depth than the thorax, brownish, rather shiny (like the head and thorax) on at least the basal tergites. Tergite 1 hairless; tergite 2 with an inconspicuous patch of short grayish hairs at each side towards the apex; tergite 3 with similar but rather fuller patches that are connected with each other by a thin band of short grayish hairs along the apex; tergites 4 and 5 also with lateral hair patches but densely and uniformly covered as well over most of their exposed surface with silvery gray hairs of rather velvety appearance, tergite 5, in addition, with longer and coarser yellowish hairs along the apex; tergite 6 with still longer yellowish to fuscous hairs than those at the apex of tergite 5 over all its exposed surface. The hairs of the sternites

width of thorax 2.5 to 3 mm.; length of forewing, including tegula, 5.25 to 6.25 mm. The larger measurements apply to the specimen from Rio Acre, Brazil.

MALE

HEAD (FIG. 5A): Smooth, with the structural characters noted for the genus *Lestrimelitta*. The lower half or more of the clypeus very abruptly declivitous at the middle and foveate with a longitudinal incised line traceable in the somewhat triangular fovea. Black except usually for some or all of the following parts, which tend to be more or less ferruginous: apex of clypeus, labrum, mandibles, malar space and lower extremity of genal area, scape in front, and occasionally the flagellum below. The head as glabrous as that of the worker, with the only erect hairs

those of the fringe, usually silvery gray, along the lower edge of the mandibles.

THORAX: Black, smooth, often nearly as shiny as the head, and with possibly somewhat the same range from sparsity to density in respect to the microscopic hairs of sericeous sheen that was noted for the worker, although for full confirmation of this impression males are needed from localities that as yet have yielded only worker specimens. A cluster of longer and coarser silvery gray hairs on the scutellum, especially posteriorly; these hairs tend to be longer in the Brazilian specimens than in the few males collected in Guatemala, Costa Rica, and Panama. Moderately long silvery gray hairs also on the under side of the thorax.

LEGS: In the limited number of males examined either wholly or predominantly reddish to reddish brown (only in the specimen from San Isidro, Costa Rica, is there some clouding of the red). The hairs of the legs on the whole sparse and short, only the outer face and posterior lateral contour of the hind tibiae (fig. 5B) being conspicuously hirsute, with long, coarse, silvery gray hairs. Rather long silvery gray hairs are present also on the hind coxae anteriorly. The hairs on the under side of the trochanters short and inconspicuous. The femora devoid or almost devoid of hairs (the specimen from San Isidro, Costa Rica, is exceptional in having moderately long whitish hairs basally on the under side of the fore femora). The fore and middle tibiae with a few silvery gray hairs along their posterior lateral contour or below it (these hairs feebly developed to absent in the Central American specimens). The inner face of the hind tibiae with the usual dense array of microscopic silvery gray hairs in contrast to the long coarse hairs on the outer face. The metatarsi with rather fine, more or less silvery gray hairs on their outer face as well as on the inner face.

WINGS: Hyaline to subhyaline, with brownish to fuscous venation and stigma, and more or less concolorous tegulae. The vestiges of the transverse cubital veins very feeble. The number of hamuli per lower wing variable from five to six. Of 14 wings examined, nine had five hamuli and five had six hamuli, an average of 5.35.

ABDOMEN: Brownish black, shiny, almost

devoid of hair over its dorsal surface, the few scattered hairs being microscopic and appressed. At least the apico-lateral area of the abdomen, however, fringed with longer hairs, which, usually on the last two or three visible tergites only, sometimes extend upward to include the fourth tergite (a specimen from Baurú, Brazil). Sternite 1 and virtually also sternite 2 devoid of hair, but the subsequent sternites increasingly silvery gray tomentose. Sternite 6, like sternite 5, with an emargination medianly at the apex (see fig. 6), its sides narrow, parallel, and extended backward for a distance about equal to the width of this sternite at the apex.

MEASUREMENTS: Length about 5.5 to 6 mm.; width of thorax about 2 mm.; length of forewing, including tegula, about 4.5 to 5 mm.

TYPE MATERIAL

Frederick Smith described *limão* from Brazil on the basis of what he believed to be the male (1863a, p. 506). The specimen designated "type" in the British Museum (Natural History) is, however, a worker, and certain details of Smith's description (for instance, "the front convex") apply to the worker rather better than they do to the male and incline me to believe that it was the worker, which in certain respects is so male-like in appearance as to prove misleading, that F. Smith had before him. I have seen no males among the F. Smith specimens of *limão* either at the British Museum (Natural History) or at Oxford.

DISCUSSION

A perusal of the descriptions of the several castes will indicate the variability in the insects from nest to nest. Perhaps a little inconsistently, I have refrained from giving varietal names to these differences, partly because of the difficulty in drawing sharp distinctions where often only a degree of gradation is manifested and partly because of the limited number of specimens available from certain regions.

The male of *limão* is unusual in having sternite 6 medianly emarginate at the apex instead of armed, as are so many male Meliponidae, with a median apical spine. Both sternite 6 and, to a more limited extent,

sternite 7 of the male of *limão* have long narrow sides, and sternite 7 at least shows rather marked variability in shape from specimen to specimen (fig. 6, D, D1, D2).

In the discussion of *Lestrimelitta* will be

found an account of the biology of *limão*, which constitutes by far the most common species of this small genus.

There seem to be no floral records for *limão*, a circumstance that lends some

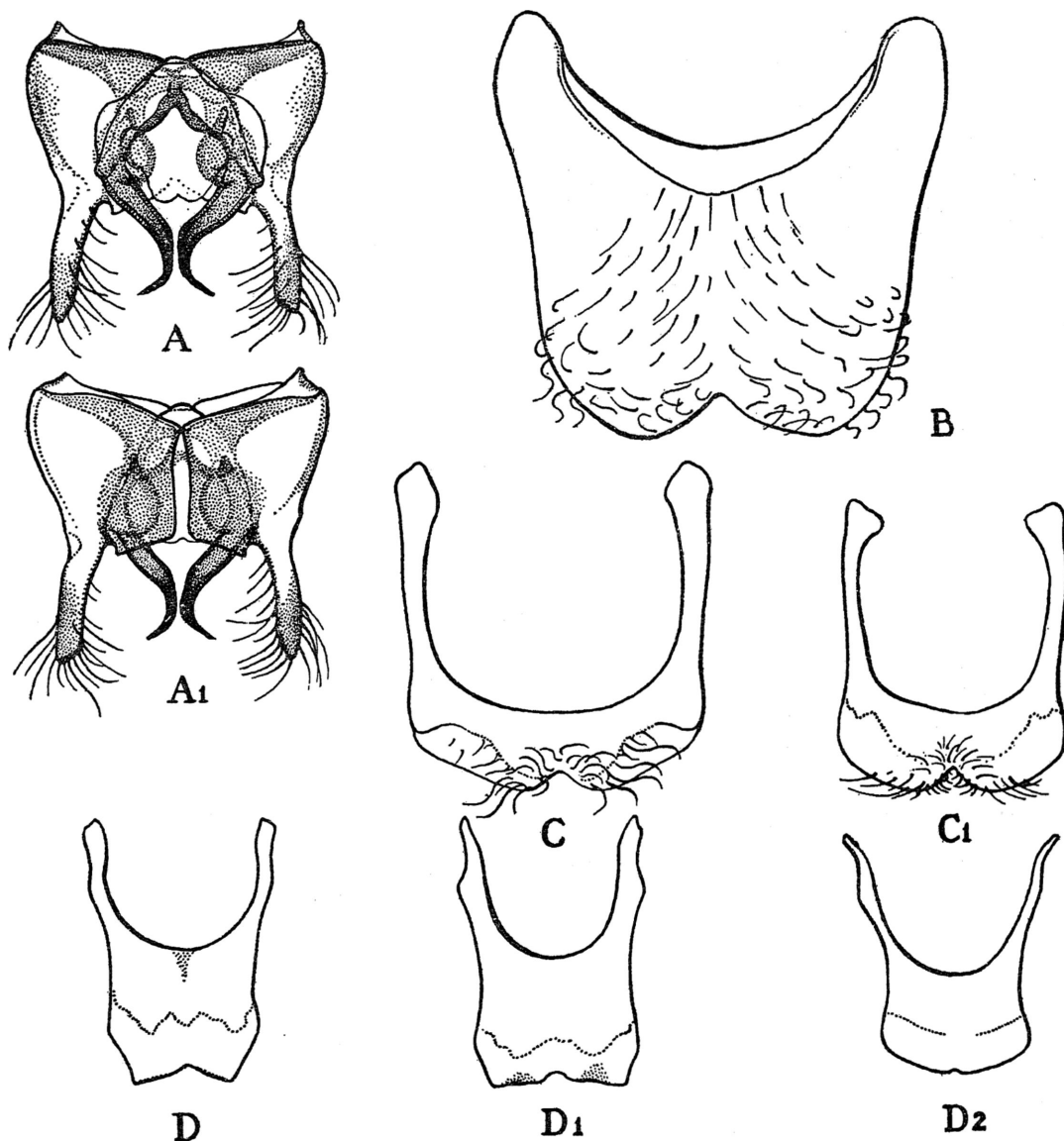


FIG. 6. Abdominal parts of the male of *Lestrimelitta limão* (F. Smith). A, A1. Dorsal and ventral views, respectively, of the genitalia (chitinized parts only) of a specimen from São Paulo, Brazil. B. Sternite 5 of a specimen also from São Paulo. C, C1. Sternite 6 of specimens respectively from São Paulo, Brazil, and San Isidro, Costa Rica. D, D1, D2. Sternite 7 of specimens from Santa Emilia Pochuta, Guatemala; São Paulo, Brazil; and San Isidro, Costa Rica. Drawings by Shirley H. Risser.

strength to the contention of those who maintain that this bee lives solely by robbery of other hives.

The bee derives its scientific name from the fact that it has a lemon-like odor. Because of this fact one is tempted to think that the bee called "limoncab" ("cab" means honey in the Maya language) is *Lestrimelitta limão*, and this inference would seem to derive support from the fact that Redfield and Villa R. (1934, pp. 49-50) in connection with the bee they allude to as "ñitcab" and "limoncab" mention that its honey is unpalatable. On the other hand, field notes supplied by the University of Yucatan that accompany specimens sent me by Dr. A. Dampf would seem to indicate that the term "limoncab" applies to *Trigona (Nannotrigona) testaceicornis* variety *perilampoides* Cresson, while *Lestrimelitta limão* F. Smith is known popularly in Yucatan as "xnuc" (pronounced shnuc), meaning "old wife." The validity of this interpretation is supported by the fact that in the State of Pernambuco, Brazil, the name "limão" is applied to *testaceicornis* because of its agreeable lemon-like smell (Ducke, 1925, pp. 343, 403), but in South America, at least, the honey of *testaceicornis* is said to be good, whereas that of *perilampoides* in Yucatan is pronounced bad.

Rodolpho von Ihering (1940, pp. 404-405) noted that in Brazil the term "iraxim," which is applied to certain members of the subgenus *Partamona*, serves also as a popular name for *limão*, although "limão" or "limão canudo" are used in the northeast. The same author noted that the term "irratim," which is conferred upon it in Rio Grande do Sul, signifies in the Tupi (or, more strictly speaking, Guaraní) language nose or funnel (tim) of honey (ira). Bertoni (1911, p. 141) in commenting on the bees of Paraguay gave as Guaraní names of *limão* the following: "eiratî," "kuañetî," "eirachî" (east of the Paraguay). "Chalatín," a corruption of "kuañetî," is a name that occurs in Corrientes (Río Argentina). "Eíra quāyetâ" (Anchieta, 1812, p. 155), "irá-tinga" (Holmberg, 1887, pp. 260-261, 266, 284-285, 287), and "coalati" (Ambrosetti, 1895, p. 699) are additional designations that have been bestowed on this little creature. In Matto Grosso, Brazil, it is called "arancín" (Silvestri, 1902b, p. 126). Another

name for this species, according to Peckholt (1893, p. 580), is "mosquito grande." Other variants of the names bestowed are listed on page 182.

In Venezuela (or at least at San Felix on the Orinoco River) the unflattering name of "culo de yegua" is given to this bee according to Mr. Vincent A. Baker, who collected it in that region. Unless it be intended as a term of contempt, this name would seem hard to explain.

DISTRIBUTION

Federick Smith (1863a, p. 506) described *limão* from Brazil, and Ducke (1916, pp. 40-41; 1925, p. 365; 1945, p. 34) listed its occurrence in the following Brazilian states on the basis of published records or specimens he had examined: Amazonas, Acre Territorium, Matto Grosso, Ceará, Goyaz, Bahia, Minas Gerais, São Paulo, Santa Catharina, Rio Grande do Sul. He also included the Misiones region of Argentina in the range on the authority of Silvestri (1902b, pp. 126-128) and Paraguay on the authority of Bertoni (1911, p. 141). I have likewise seen specimens from Paraguay.

The range is, however, far more inclusive, and Friese (1931, p. 2) indicated that *Lestrimelitta* (and presumably this may be interpreted as applying especially to the more common species *limão*) is found from Mexico to northern Argentina.

In the collections before me there are specimens of *limão* from the following localities:

MEXICO: Northern Yucatan (Gaumer), Chichen-Itza, Aug. 28, 1946 (H. F. Schwarz).

GUATEMALA: Santa Emilia Pochuta, 1000 meters, Feb.-March, 1931 (J. Bequaert), male.

COSTA RICA: Alajuela (A. Alfaro): San Isidro, Aug. 7, 1937 (A. Alfaro), including males.

PANAMA: Bugaba (Champion), including males; Bella Vista, Feb. 21, 1923 (W. M. Wheeler); Old Panama, March, April, May, July, Dec. (C. D. Michener).

CANAL ZONE: Barro Colorado Island, Feb. 18, 1929 (C. H. Curran), Nov. 14, 1930 (E. I. Huntington and H. F. Schwarz), Nov. 15, 1930, on excrement (E. I. Huntington and H. F. Schwarz), Feb. 27, 1933 (H. F. Schwarz), Apr. 1-10, 1934 (J. C. Bradley), Aug. 8, 1934 (O. E. Shattuck).

COLOMBIA: Muzo, Dept. of Boyacá, 900 meters, June 20-30, 1936, and July, 1936 (J. Bequaert).

VENEZUELA: Caripito, Dec. 19, 1943 (R. Mado), robbing honey from hive of honeybee

according to C. H. Ballou. San Felix, State of Bolivar, July 1, 1946 (V. A. Baker).

TRINIDAD: May, 1935 (FitzGerald), and (F. W. Urich); San Rafael, July 26, 1945 (R. G. Donald), including males and virgin queens.

BRITISH GUIANA: Northwest District: Yarikita, Feb., 1931 (J. G. Myers); Mabaruma, March, 1931 (J. G. Myers); Essequibo River (J. Ogilvie), male.

ECUADOR: Tena, March 4, 1923 (F. X. Williams).

PERU: San Ramon, Valle de Chanchamayo, 800 meters, 1939, No. 151, Feb. 5, 1940, and Feb. 12, 1940 (W. Weyrauch).

Clypeus not sharply foveate at the apical middle, depressed area wide but shallow, flat. Hairs on head and especially on the thorax dense but for the most part also very short. Thorax finely but densely tessellated. Abdomen clear red, with rather long hairs, especially on tergites 3 to 6.

HEAD (FIG. 7A): With the structural characters noted for the genus *Lestrimelitta*. The lower half of the clypeus not abruptly declivitous as in *limão*, rather more widely but also more shallowly depressed over the middle area from the apex upward towards

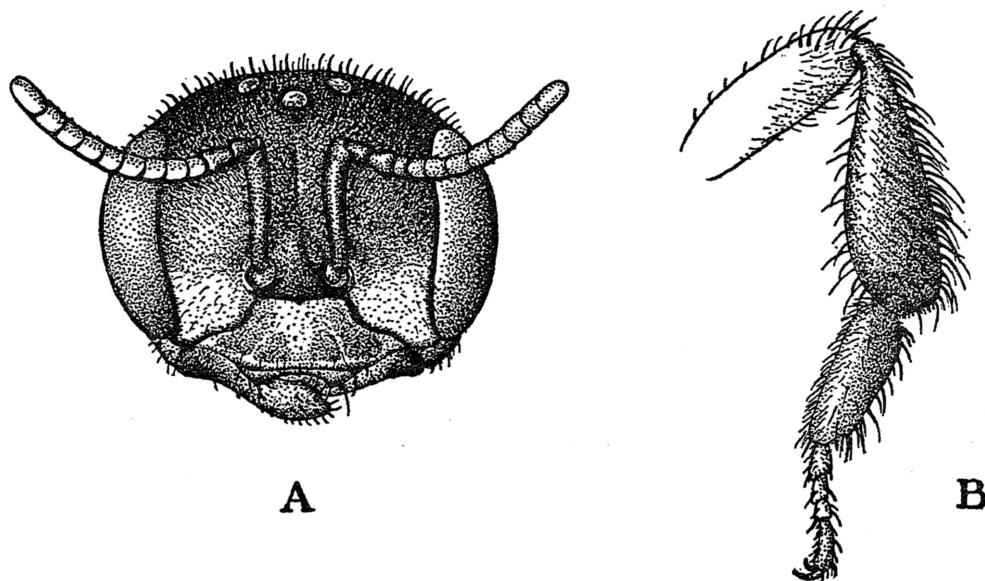


FIG. 7. Worker of *Lestrimelitta ehrhardti* Friese. A. Head. B. Tibia and tarsal joints of hind leg. Drawings by Shirley H. Risser.

BRAZIL: State of Amazonas: trail (Cameron). Acre Territorium: Rio Acre, 1902, a queen. State of São Paulo: Baurú, 1897, 1899 (von Ihering), including males; Jundiáhy.

PARAGUAY: Without locality designation, a queen and workers.

***Lestrimelitta ehrhardti* Friese**

Lestrimelitta ehrhardti FRIESE, 1931, pp. 13-14.
Lestrimelitta ehrhardti, SAPPER, 1935, p. 184.

WORKER¹

DIAGNOSTIC CHARACTERS: Clypeus and lower half of sides of face broadly maculated, for the most part ivory colored (or yellow).

¹ Description based on a single specimen from Uberaba, State of Minas Gerais, Brazil.

the base. Black but with the following well-developed and conspicuous maculations: two large, rounded, ivory-colored maculations, one on each side of the clypeus, completely filling the space between the clypeus and the eye and extending upward beyond the base of the clypeus to about the upper level of the antennal sockets. (In Friese's description these maculations are referred to as being yellow, and this may apply to the specimen not in the American Museum.) The clypeus itself also more or less ivory colored but suffused to some extent with ferruginous (in Friese's description only the lower half of the clypeus is referred to as maculated with yellow). The strongly bitubercular labrum deep

red as are the mandibles except for their black basal prominences and their apex narrowly margined with black. The antennal sockets ferruginous, the scape narrowly ferruginous at the apex, and the flagellum more or less cloudy ferruginous on its under side. As in *limão*, the longest hairs, mainly silvery gray, are in the fringe along the lower margin of the mandible, but in addition there are grayish to darker hairs over the rest of the head and, though very short, these hairs are rather dense on at least the front, vertex, and genal area, being relatively sparse only in the maculated areas. The chitin dulled by the presence of the hairs but, when these are removed, revealing a smooth shiny surface (in Friese's description the head is said to be "dulled by fine sculpture").

THORAX: Black or blackish, without pale maculations, and, except for the bare shiny dorsal and middle region of the propodeum, very densely covered with dark grayish to brownish tomentum. In addition there are erect hairs, which are grayish to blackish on the scutellum and a little longer than the similar black or blackish hairs anteriorly on the mesonotum, which in turn are notably longer than the rather short erect gray hairs on the mesopleura. In further contrast to *limão*, the chitin of the thorax of *ehrharti* is not smooth but finely tessellated.

LEGS: Predominantly reddish brown on the basal joints to the inclusion of the femora, which, however, tend to be cloudy or sooty towards the apex. The tibiae and metatarsi, on their external face at least, wholly or almost wholly black but the small joints of the tarsi rather bright ferruginous (Friese described the legs as blackish brown). The hairs silvery gray to cream colored on the coxae and trochanters beneath, being especially dense on the under side of the middle trochanters. A dense fringe of very microscopic pale hairs is traceable on the under side of the femora, running the length of the joint, and equally microscopic concolorous appressed hairs occur, but inconspicuously, over other areas of the fore and middle femora, which are much less hirsute, however, than are the hind femora on at least their outer or anterior face, this face being rather densely covered with dull grayish or yellowish to darker erect hairs. The external face of the fore and middle

tibiae with for the most part only microscopic appressed hairs that have a sericeous sheen; both the fore and middle tibiae, in addition, with black erect hairs along their posterior lateral margin and, in the case of the middle tibiae, likewise on the under side of the joint. The outer face of the hind tibiae (fig. 7B) not hairless and strongly shiny as in *limão*, but with its surface somewhat dulled by the presence of microscopic appressed hairs and ultra-delicate tessellation; the anterior and posterior lateral contours of the hind tibiae fringed with simple black hairs, those of the posterior fringe being the denser and longer; the inner face of the hind tibiae rather densely covered with silvery gray microscopic hairs. The several metatarsi with their outer face inconspicuously covered with appressed hairs, and with erect brownish hairs, in addition, fringing them anteriorly and posteriorly, but the posterior hairs a little the longer although themselves short. Metatarsal brushes pale golden.

WINGS: Subhyaline, even a little milky, with brownish venation and stigma; particularly the first transverse cubital vein a little more strongly developed than in *limão*. The tegulae fuscous, with a small reddish pupil. Number of hamuli per lower wing, in the only specimen available for examination, five.

ABDOMEN: Rather clear reddish, smooth and moderately shiny, with minute scattered punctures traceable here and there where the hairs emerge. These abdominal hairs, much more abundant and longer than those of *limão*, are present on all the tergites although relatively short on tergite 1, which they cover even to the edge of the basal depression, and on tergite 2, where they are largely confined to the apical half and sides. The apical half of the subsequent tergites with the hairs long, semi-erect, and of even distribution and growth. The hairs seem gray or black on the tergites, depending on the angle from which they are viewed. The hairs on the ventral side of the abdomen are gray and abundant but no longer, if anything shorter, than the hairs on tergites 4 to 6. (Friese refers to occasional hairs on the ventral side of the abdomen as well as those of the dorsal side as black but adds that on segment 6 the hairs are brown.)

MEASUREMENTS: Length about 5.75 mm.; width of thorax about 2.25 mm.; length of

forewing, including tegula, about 5.75 mm. (Friese gives the length as 7 mm. and the width as 2 mm.)

QUEEN

UNKNOWN.

MALE¹

HEAD (FIG. 8A): Feebly tessellated, with the structural characters noted for the genus *Lestrimelitta*. The middle region of the

and to some extent over the clypeus) with short, dull grayish to brownish black erect or semi-erect hairs (the dark hairs are most in evidence on the vertex); the hairs fringing the mandibles below are pale to slightly ferruginous.

THORAX: Faintly tessellated, black, and notably hairy, all parts except the smooth shiny dorsal aspect of the propodeum being covered for the most part with short grayish to brownish hairs of rather uniform density,

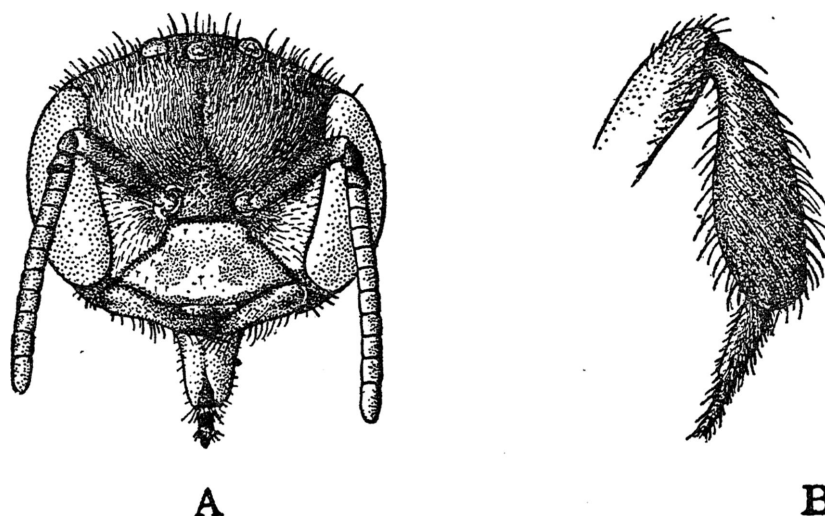


FIG. 8. Male of *Lestrimelitta ehrhardti* Friese. A. Head. B. Tibia and tarsal joints of hind leg. Drawings by Shirley H. Risser.

clypeus with a rather wide subtriangular depression extending from near the base to the apex and in which is traceable an incised longitudinal line. Black but with the following ivory-colored maculations: mandibles (except blackish apical edge and basal prominence), labrum, clypeus (except for two faintly brownish spots), subtriangular side-facial maculations filling the space between the clypeus and the eye and terminating about halfway up the eye, their inner edge emarginated with blackish at about the level of the antennal sockets. The antennal sockets ferruginous as is also narrowly the base of the scape; the scape otherwise black and the flagellum only barely less blackish below than above. The head covered rather densely (especially over the front, vertex, and genal area

those of the scutellum longer and somewhat intermixed, especially posteriorly, with blackish hairs. The grayish hairs on the under side of the thorax longer than the hairs on the mesonotum and mesopleura.

LEGS: With the coxae, trochanters, under side of femora, inner face of tibiae, and the small joints of the tarsi red or predominantly red, but the upper side of the femora, the outer face of the tibiae (except in some cases a small reddish basal and apical spot), and the outer face of the metatarsi more or less fuscous. The hairs of the leg rather abundant even if short over most of the joints, being sparsest on the inner and the upper face of the fore and middle femora. The hairs on the trochanters below, the microscopic hairs fringing the femora below, and the hairs anteriorly on the hind coxae silvery gray. The other hairs dull grayish to brownish, a little longer on the posterior lateral contour of the

¹ Description based on a single specimen from São Paulo, Brazil.

fore and middle tibiae and over the outer face and posterior lateral contour of the hind tibiae, although the hairs on the hind tibiae (fig. 8B) are not nearly so long as are the hairs of the corresponding joint in the Brazilian representatives (males) of *limão*. The inner face of the hind tibiae with the usual

moderately shiny, with minute scattered punctures traceable here and there, coinciding for the most part with the points of emergence of the hairs. These hairs, abundant and grayish brown or (viewed from certain angles) even blackish, are present on the exposed parts of all the tergites, encroaching

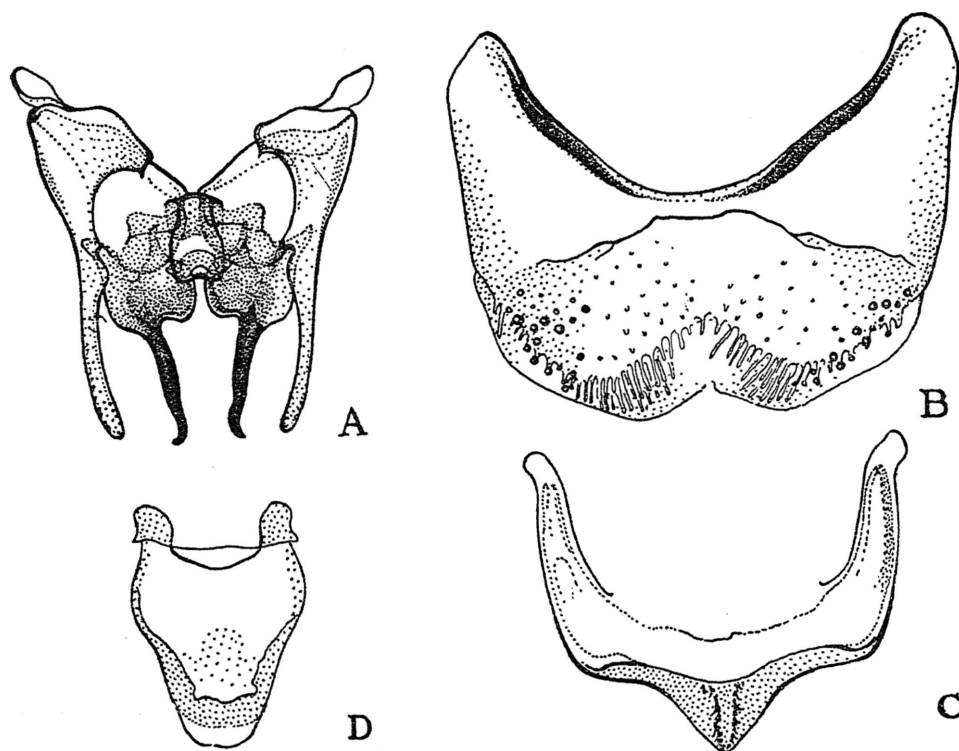


FIG. 9. Abdominal parts of the male of *Lestrimelitta ehrhardti* Friese. A. Genitalia (somewhat mutilated). B, C, D. Sternites 5, 6, and 7, respectively. All based on a specimen from São Paulo, Brazil. Drawings by Shirley H. Risser.

dense array of microscopic silvery gray hairs. The inner face of the metatarsi with rather fine hairs that tend to have a light golden tinge.

WINGS: Subhyaline, even a little milky, with brownish venation and stigma; particularly the first transverse cubital vein a little more strongly developed than in *limão*. The tegulae fuscous, with a small, faintly ivory-colored pupil. Number of hamuli per lower wing, in the only specimen available for examination, five.

ABDOMEN: Rather clear reddish, with a transverse hair-fine stripe of black traversing each of the several basal tergites, smooth and

even upon the basal depression of tergite 1, but tend to be longer on the apical tergites than on the basal. All of the sternites likewise with hairs, which are silvery gray and on the whole shorter than the hairs of the dorsal side of the abdomen. Sternite 5 (fig. 9B) emarginate medianly along the apex; sternite 6 with a stout median spine (fig. 9C).

MEASUREMENTS: Length about 6.5 mm.; width about 2 mm.; length of forewing, including tegula, about 5.75 mm.

TYPE MATERIAL

Friese (1931, p. 13) described *Lestrimelitta ehrhardti* on the basis of two workers collected

by Draenert at Uberaba, State of Minas Gerais, Brazil, at 800 meters. One of these two specimens was acquired by the American Museum of Natural History. The male allotype, from São Paulo, Brazil, is likewise in the collection of the American Museum of Natural History.

DISCUSSION

This rare insect is, as Friese pointed out, indubitably a *Lestrimelitta*, sharing the characters of that subgenus to the inclusion in both worker and male of the relatively large third joint of the antennae (second of the flagellum). In some of the details of the description of the worker, my own interpretation of the characters differs in details, such as that of coloration, from Friese's summation. However, it may be that these differences are explainable by the fact that the type material of Friese consisted of two workers and that Friese concentrated his attention on the worker that was retained by him, while my examination was necessarily confined to the worker that was acquired from him. At any rate, it seems in order to include the divergent interpretations in the above description of the worker.

What I believe to be the male of *ehrharti* is here described for the first time. The specimen is unfortunately a unique, and its interpretation lacks the support, therefore, ordinarily derived from the presence of accompanying workers. Because of the specimen's distinctive structure, especially the structure of the head, with the disproportionately long third antennal joint, I believe it belongs in *Lestrimelitta*, and because of its sculpturing, maculations, and pilosity it seems to me assignable to *ehrharti*. It should be emphasized, however, that although in so many ways like the male of *limão*, this putative male of *ehrharti* has abdominal sternites that are rather at variance with those of *limão*, as a comparison of the drawings (figs. 6, 9) of sternites 5 to 7 of each species will indicate.

Although the worker of *ehrharti* differs from the corresponding caste of *limão* in such structural details as sculpturing and the form of the clypeus, both worker and putative male of *ehrharti* will be most readily distinguished from the worker and male of

limão by their greater hairiness, the ivory maculation of the lower one-half of the face, and the red abdomen.

DISTRIBUTION

Known only from the Brazilian States of Minas Gerais and São Paulo and as yet reported from only a single locality in each of these states.

TRIGONA SUBGENUS TRIGONA JURINE

Trigona JURINE, 1807, pp. 245-246.

TYPE SPECIES: *Apis amalthea* Olivier.

WORKER

DIAGNOSTIC CHARACTERS: Especially differentiated by the following combination of characters: Chitin smooth, without or virtually without sculpturing, the shininess of the surface dulled only, if at all, by the presence of hairs. The mandible along its apex either five-toothed or four-toothed or with three teeth and a strong inner angle that is subtooth-like, never edentate along the anterior one-half of its apex, although there are sometimes thin septa of chitin uniting the teeth. The external face of the middle tibiae usually with plumose as well as simple hairs (poorly developed to sometimes absent in *hypogaea*), and such plumose hairs also fringe the posterior lateral margin of the hind tibiae. The hind tibiae more or less clavate and somewhat longer than the combined length of the hind femora plus the hind trochanters. The inner face of the hind metatarsi with a smooth, bristleless, usually silvery gray sericeous and more or less oval-shaped area on the basal one-third to one-half that is in sharp contrast with the bristle-covered area apical to it [all workers of the subgenus *Trigona* and the males so far as known have this character, but of the New World representatives of other subgenera only the workers of *Trigona* (*Tetragona*) *jaty* F. Smith, *buchwaldi* Friese, and *pfeifferi* Friese share this distinction]. A somewhat crescentic depression usually traceable along the apex of tergite 1 and sometimes also along the apex of tergite 2 of the abdomen.

HEAD: Wider than long, extending to each side somewhat beyond the outer rim of the tegulae. The facial quadrangle wide, the distance between the eyes at a level just below

the anterior ocellus variably a little more or a little less than, or about equal to, the distance from the middle ocellus to the apex of the clypeus. The eyes always at least somewhat convergent below, usually rather strongly so. The clypeus twice to fully thrice as wide at its widest as it is long; its sides subparallel over the basal half or more, and abruptly divergent on the apical half; its apico-lateral extremities form an acute angle; its apex is widely truncate along the middle with a recession towards each of its extremities. The face of the clypeus is either flat or slightly arched, and of smooth surface throughout, medianly channeled, or apically foveate. The mandibles overlapping, widest at the base and apex, slightly narrowed towards the middle, the apical edge toothed from end to end, or with at least three teeth on the outer half of the apex and a strong angle at the inner extremity of the apex. The malar space much longer towards its outer extremity (near the outer angle of the base of the mandible) than at the inner extremity (near the inner angle of the base of the mandible), usually approximating, when measured midway between these limits, the width of the flagellum but sometimes attaining a length equal to almost twice the width of the flagellum (*trinidadensis*). The labrum simple or (more rarely) with two feeble tubercles. The supraclypeus barely to sometimes emphatically more prominent than the clypeus, subtriangular in contour, longer than wide, its summit connected with the middle ocellus by a shallow fossa that is usually more easily traced below than above. The middle ocellus barely anterior to the lateral ocelli, somewhat depressed, sometimes round but more often with its transverse axis greater than its longitudinal. The lateral ocelli raised and tilted each towards the nearest compound eye. The distance between the lateral ocelli subequal to, or in other cases only about two-thirds as great as, that separating each lateral ocellus from the nearest compound eye. A more or less developed carina, often feeble, behind the ocelli and about coextensive with them. The hairs of the head are of two kinds: (1) microscopic silvery gray¹ appressed hairs that are particularly

dense (pruinose) on the upper two-thirds of the genal area, nearly as dense on the sides of the face, usually a little less so (sometimes even absent) on the front and the clypeus; (2) longer erect hairs, variable according to species from black to fulvous and variable likewise in length but usually increasing in length over the front upward and attaining usually their greatest length on the vertex, lower margin of mandibles, and lower one-third of genal area. The flagellum about twice the length of the scape.

THORAX: Smooth. The mesonotum, measured along the base, where it is widest, a little wider than long, but the combined length of the mesonotum and scutellum, which is separated from the mesonotum by a deep fossa, greater than the greatest width of the mesonotum. The scutellum slightly arched over its upper surface, its posterior contour rounded and entire and barely or not at all impinging upon the medianly hairless and shiny propodeum. The hairs of two kinds: (1) short and more or less tomentose (sometimes appressed, especially on the mesonotum); and (2) erect simple hairs ranging from fulvous and even silvery gray to black according to the species, and of variable length according to the area of the thorax on which they occur. The tomentum occurs over the dorsal surface and on the sides of the thorax to the inclusion of the sides of the propodeum. The erect simple hairs occur in all of these areas likewise. Those on the scutellum are longer than those on the mesonotum, often quite strikingly so. The hairs on the mesopleura tend to increase somewhat in length downward, and become conspicuously long on the under side of the thorax. A semicircular fringe of tomentose hairs partly encircles the tubercles and is supplemented by a densely tomentose patch immediately below and mostly posterior to the tubercles; these tomentose hairs frequently paler than those of adjacent regions.

LEGS: Progressively longer from the fore pair to the hind pair, the hind pair usually tending to exceed (not so in at least *compressa*) the combined length of the head, thorax, and abdomen, although the degree to which the abdomen is telescoped makes generalization as to relative length impossible. The tibiae of the fore legs shorter than

¹ In some lights these hairs may now and then appear slightly olivaceous.

their femora; those of the middle legs about the same length as their femora; those of the hind legs a little longer than the combined length of their femora and their trochanters. The contour of the hind tibiae more or less clavate, in many species (but not in all) sub-tooth-like or angulate where the posterior lateral contour meets the apical contour. The outer face of the hind tibiae more or less depressed on its apical one-third to two-fifths, especially posteriorly. The under side of the hind tibiae rather declivitous anteriorly (a region over which the hairs are relatively long and simple). This declivitous area merges into a raised plateau-like area that occupies virtually the entire downward extent of the middle region of the under side of the joint and is covered densely with thick but exceedingly short silvery gray bristles that are a continuation of a similar dense patch of microscopic bristles usually traceable on the inner side of the apex and upward of the hind femora. The plateau-like area is succeeded posteriorly by a sharply contrasted and abruptly flattened area (of variable width from species to species) that extends nearly from the base to the apex of the under side of the joint and is much wider towards the apex than the base. The hind metatarsi of variable width from species to species as compared with the width of the hind tibiae; these metatarsi, as a rule, slightly convex along their posterior contour to subparallel-sided, usually a little convergent at the base but rarely with the contrast between the narrowed base and widened apex so great that the metatarsi appear subtriangular, and either square-cut to rounded at the apex posteriorly or with a somewhat acute angulation. The hairs usually fairly abundant on all the joints except the femora, where they are for the most part sparse, short, and inconspicuous. The hairs of the coxae as a rule longer and denser anteriorly than posteriorly (particularly does this apply to the hairs of the hind coxae). The hairs of the trochanters largely or wholly confined to the under side of the joint, and more tomentose on the under side of the middle trochanters than on the fore or even the hind pair. The sparse, short, simple hairs of the femora are, at least in the case of the fore and middle pair, confined largely to the under side. A dense fringe of

very microscopic pale tomentose hairs often traceable on the under side of at least the middle femora. The hairs of the fore and middle tibiae and particularly the hairs of the metatarsi tend to be longer along the posterior lateral contour than along the anterior lateral contour of these joints. The simple hairs of the external face of the middle tibiae are distinctly longer than those of the external face of the front tibiae; on the external face of the middle tibiae the simple hairs are usually abundantly intermixed with plumose hairs, which frequently extend to the basal part of the external face of the middle metatarsi. The simple hairs increasingly long towards the apex of the under side of the middle tibiae. The simple hairs on the external face of the fore and middle metatarsi and posteriorly on these joints longer than the hairs on the external face of front tibiae and longer than, if not so dense as, most of the hairs of the metatarsal brushes of the fore and middle legs. A thin fringe of unbranched hairs along the anterior lateral margin of the hind tibiae; the fringe along the posterior lateral border is much denser and composed predominantly of plumose hairs with scattered unbranched hairs more or less thinly interspersed. Simple and usually intermingled plumose hairs present over the outer face of the hind tibiae, more particularly so on the basal one-half; these hairs usually erect and long. The declivitous area anterior to the plateau-like median area and to a less extent the flattened posterior rim of the under side of the hind tibiae have semi-erect simple hairs. Simple hairs fringe the sides of the hind metatarsi and are present more or less thinly also over their external face. The under side of the hind metatarsi characterized especially by a smooth, bristleless, more or less silvery gray sericeous area of suboval contour (sometimes the hairs are much discolored by adherent foreign matter) occupying the basal one-third to one-half of the joint and in sharp contrast with the bristle-covered apical one-half to two-thirds of the joint. Small joints of tarsi moderately hairy; claws simple with a well-developed pulvillus.

WINGS: With the first discoidal cell of somewhat variable length when compared to the marginal cell; in the rather aberrant *compressa* about as long as the marginal cell but

usually only about seven-tenths to a little over eight-tenths as long. The transverse cubital veins usually only faintly or not at all traceable but sometimes relatively strong (more especially in *ruficrus*). The upper half of the first transverse cubital vein tends to be more clearly demarked than the lower half, while the second transverse cubital is of about the same degree of intensity or vagueness throughout. The marginal cell in some cases approximately closed, but in other forms (more particularly those with milky wings) the marginal vein tends to fade out briefly before its apex attains the edge of the wing. The number of hamuli per lower wing relatively small, rarely as few as four, very exceptionally as many as eight, usually five or six depending on the species.

ABDOMEN: Usually telescoped, of comparable width to the thorax and trigonate but in one instance (*compressa*) narrow, elongate, and ridged dorsally. The chitin smooth and sculptureless or virtually sculptureless. Tergites 1 and 2 bare or with usually merely a few inconspicuous hairs (as a rule appressed) along the apex of tergite 2 and extending also sometimes up the sides. The apex of tergite 3 sometimes only inconspicuously covered with hair, but the apical half of tergites 4 and 5 and most of tergite 6 (or in the case of *compressa* usually only 5 and 6) with hairs of greater length that give to this frequently telescoped part of the abdomen a more or less continuously hairy appearance in contrast to the relatively glabrous aspect of the basal part of the abdomen. Tergite 1 with a crescentic depression along its apex (sometimes a little difficult to trace in some specimens, particularly those of small stature). Tergite 2 also depressed, although usually more shallowly, along its apex. The ventral aspect of the abdomen usually more hirsute than the dorsal, the several sternites having hairs over their apices that, long in the middle region, grade into shorter hairs or sericeous patches to each side.

QUEEN

DIAGNOSTIC CHARACTERS: The number of known queens within the subgenus *Trigona* is too limited to justify final conclusions regarding the characters common to the queen, and the following summary should be read with

caution. It would seem likely, however, from an examination of the six species that have the royal caste available for study that the dentition of the mandible, although less strongly demarked than in the worker, is nevertheless more or less characteristic of the female of this subgenus. Other characters relied upon, in combination with the dentate mandibles, to separate the worker of subgenus *Trigona* from the worker of other subgenera of *Trigona* do not apply to the queen: the outer face of the middle tibiae is devoid or virtually devoid of plumose hairs, and such hairs are also without representation along the posterior lateral contour of the hind tibiae; there is no differentiated sericeous area at the base of the inner face of the hind metatarsi.

HEAD: Relatively smaller, when compared to the width of the thorax, than that of the worker.¹ The eyes usually shorter than those of the worker, distinctly narrower, more nearly parallel to each other, with little convergence below, now and then sparsely and inconspicuously hairy. The malar space much longer than in the worker. The mandibles at least indistinctly and sometimes rather strongly toothed. The clypeus usually a little more prominent than that of the worker and not apically appressed at the middle and without a median longitudinal fossa even in species in which the clypeus of the worker is thus characterized. The labrum usually simple, but with two tubercular prominences in species in which the labrum of the worker is thus equipped. The ocelli distinctly more remote from the compound eyes than is either lateral ocellus from its fellow. The distribution, length, and quality of the hairs very different from species to species; the coloration of the hairs, even in species where the erect facial hairs of the worker are black, frequently grayish to now and then fuscous. The

¹ The relationship in size of body parts between the queen and the conspecific worker differs somewhat from species to species in the case of the specimens before me. The representative of the royal caste of *amalihea* is particularly large when compared to the small worker, and compares not unfavorably in size with the queen of *trinidadensis*, the worker of which dwarfs the worker of *amalihea*. It is impossible to conclude on the basis of the limited number of specimens before me whether the size of the queen in a given species is as nearly constant as that of the worker caste.

coloration of the head approximating that of the worker.

THORAX: In all known instances wider than that of the worker. The length of the mesonotum plus scutellum usually a trifle greater than the width of the mesonotum measured along its base. The length and abundance of the erect hairs very variable from species to species, but the hairs on the scutellum in all instances longer, sometimes strikingly longer, than the hairs of the mesonotum. The coloration of the hairs in species that in the worker have the erect hairs black, at most partly fuscous with gray frequently predominating. The coloration of the chitin approximating that of the worker. The middle area of the propodeum glabrous and shiny like that of the worker and male.

LEGS: More robust than those of the worker. The hind tibiae not so distinctly clavate as those of the worker, their anterior lateral contour straight rather than (as in the worker) slightly concave, their posterior lateral contour only feebly convex (more strongly so towards the base) with less disparity between the wider apex and narrower base than is the case in the worker; the flattened area posteriorly on the under side of the hind tibiae relatively narrow and less contrasted with the median raised area (the area covered with microscopic silvery gray bristles) than is the case in the corresponding parts of the worker. The hind metatarsi at their widest somewhat more than one-half the width of the associated tibiae at their widest, and as a rule, tapering slightly towards the apex, reversing in this respect the condition in the worker, whose hind metatarsi tend to be rather wider at the apex than at the base. The length of the hind metatarsi of the queen usually (not always) a trifle greater than the combined length of the small joints of the tarsi. The hairs of the legs vary in length and quality from species to species. Differing sharply from the worker of *Trigona*, the queen lacks, or virtually lacks (at least in the limited number of species before me), the plumose hairs on the outer face of the middle tibiae and along the posterior lateral contour of the hind tibiae, while equally noteworthy is the absence of the differentiated sericeous oval area at the base of the under side of the hind metatarsi. As in the worker,

the tibiae tend to be more hirsute than the femora, the inner (posterior) face of which in particular is rather glabrous. The hairs tend to be a little longer on the outer face of the middle tibiae than on the outer face of the fore tibiae, but the contrast is far less marked than in the corresponding joints of the worker; the outer face of the hind tibiae has hairs that are longer than those of the like area of the middle tibiae, and these hairs cover the joint from base to apex. The hairs are longer on the posterior lateral contour than on the anterior lateral contour of the metatarsi and small tarsal joints, but sometimes the difference in length is only very slight (*amalthea*). The coloration of the hairs in species in which the worker has black hairs is more often grayish to fuscous than black. The chitin of the legs of these darker species is apt to be far more invaded by reddish or brownish than is the case in the chitin of the head and thorax.

WINGS: Short, the forewings sometimes actually shorter, in other cases actually longer, than those of the worker, but always they are relatively shorter when the respective sizes of the queen and of the worker are considered. In no case does the tip of the forewing of the queen extend so far back as the apex of the abdomen, whereas in the worker and in the male the forewing as a rule projects considerably beyond the anal extremity of the bee. Number of hamuli, in the few specimens available for examination, ranges from five to seven.

ABDOMEN: In all instances (even those of virgin queens) wider than the thorax and usually distinctly longer than the combined length of the head and thorax. The first four tergites approximately horizontal in position, the fifth and particularly the sixth tergite more vertical. Some of the tergites seemingly rather finely and densely punctured, the punctures corresponding with the points of emergence of the hairs. The hairs of the tergites differ in their length, character, and distribution from species to species, but they tend to be gray even in species the worker of which has black hairs, and always they are dense on at least tergites 3 to 6. The ventral side of the abdomen with more or less erect hairs on the apical one-half of the sternites, those on sternite 6 shorter and denser.

MALE

DIAGNOSTIC CHARACTERS: At least among New World species the male of subgenus *Trigona* is separable from that sex of all the other subgenera so far as known by the presence, at the base of the inner face of the hind metatarsus, of a more or less distinct sericeous patch of flattened hairs that is more or less in contrast to the semi-erect hairs over the more apical part of the inner face of the joint.

HEAD: Wider than long, extending to each side somewhat beyond the outer rims of the tegulae. The facial quadrangle narrower (usually much narrower) than that of the worker, the distance between the anterior ocellus and the apex of the clypeus always at least a little greater, and in some species emphatically greater, than the distance between the compound eyes at a level just below the anterior ocellus. The eyes wider than in the conspecific worker (the difference is only slight in *dallatorreana*) and more emphatically convergent below. The clypeus relatively narrower and longer than that of the conspecific worker, the length being about one-half to three-fourths that of the distance from one lateral extremity of the clypeus to the other; its sides subparallel over the basal half or more, and more or less divergent over the apical half (but not so sharply so as in the conspecific worker); the apico-lateral extremities acute to, in some species, almost rectangular (never so sharply acute as in the conspecific worker); the apex widely truncate along the middle with a recession towards each of its extremities. The face of the clypeus may approximate the flat, be slightly arched, of even surface throughout, feebly channeled, or barely depressed at the apical middle, but these irregularities of surface when they occur are less than in the conspecific worker. The mandibles, when retracted, overlap each other even if in some cases only slightly; their apex either very narrow and rather bluntly pointed or with an oblique truncation inward, which is, however, edentate or with only feeble vestiges of teeth. The malar space notably shorter than in the conspecific worker, sometimes obsolete or nearly obsolete at its inner end (near the inner angle of the base of the mandible) but more developed towards its outer end (near the outer angle of the base of the mandible); relatively long in at least

trinidadiansis. The supraclypeus usually at least a little more prominent than the clypeus, subtriangular in contour, higher than wide, its summit connected with the middle ocellus by a shallow fossa that is usually more easily traced below than above. The middle ocellus barely anterior to the lateral ocelli, somewhat depressed, usually relatively small, sometimes round but more often with its transverse axis greater than its longitudinal. The lateral ocelli raised and tilted each towards the nearest compound eye. The distance between the lateral ocelli sometimes only barely greater than that between a lateral ocellus and the nearest compound eye (*nigerrima* and *trinidadiansis*) but in most cases emphatically greater. A carina, even if sometimes very feeble, behind the ocelli. The hairs of the head are of two kinds: (1) microscopic silvery gray appressed hairs that are particularly dense (pruinose) on the upper two-thirds of the genal area, nearly as dense on the sides of the face, usually a little less so (sometimes even absent) on the front and on the clypeus; (2) longer erect hairs, variable according to species from black to fulvous, and variable likewise in length. In all of the species from which the male is known this sex has at least some erect or semi-erect hairs on the clypeus (even in species where the worker lacks such hairs) and often these hairs are rather abundant and rather long. Frequently the hairs of the clypeus exceed in length those of the front. The longest hairs of the head are those on the vertex and those fringing the mandibles below. Also long are as a rule the hairs on the labrum and on the lower one-third of the genal area. The flagellum three to four times as long as the scape, which is shorter than in the conspecific worker. The third joint of the flagellum viewed from below notably longer than the combined first and second joints.

THORAX: Smooth, usually a little longer than in the conspecific worker, the measured distance from the base of the mesonotum to the apex of the scutellum showing as a rule a difference of nearly one-tenth to one-fifth in the two castes.¹ The length of the mesonotum

¹ I have found this difference of thoracic length to hold for all of the species of subgenus *Trigona* except *dallatorreana*. The specimen that I interpret as the male of *dallatorreana* is unaccompanied by workers. It is possible that, were the workers from the same nest

plus scutellum greater, usually notably greater, than the width of the mesonotum at its base. The mesonotum and scutellum separated by a deep fossa. The scutellum slightly arched over its upper surface, its posterior contour rounded and entire and barely or not at all impinging upon the medianly hairless and shiny propodeum. The hairs of the thorax approximate in character and distribution those described for the worker, but the hairs of the mesonotum in some species very short, sparse, and inconspicuous (especially is this the case in the males before me of *pallida*, *amapana*, *chanchamayoënsis*, and *compressa*), while in the male of *dallatorreana* the hairs of the mesonotum are fully as long as, or longer than, those of the scutellum.

LEGS: Progressively longer from the fore pair to the hind pair. The tibiae of the fore legs distinctly shorter than their femora; the tibiae of the middle legs almost as long as their femora; the tibiae of the hind legs about equal to (*pallida*, *amapana*, *chanchamayoënsis*), or a little greater than, the combined length of the hind femora and trochanters. The hind tibiae wider at the apex than at the base, in many instances not much narrower than those of the conspecific worker, being narrowest in *pallida*, *chanchamayoënsis*, and *amapana*, and widest in *trinidadensis*. The contour of the hind tibiae more or less clavate, but the apical margin and the posterior margin confluent and hence either without or virtually without an angulation (usual in many of the workers) where the two margins meet. The outer face of the hind tibiae convex anteriorly, more or less flattened posteriorly, in some forms (*pallida*, *chanchamayoënsis*, *amapana*, *fulviventrís*, *compressa*) even somewhat concave towards the apex posteriorly. The under side of the hind tibiae rather declivitous anteriorly (a region in which the hairs tend to be relatively long and simple). This declivitous area merges

into a raised plateau-like area that occupies virtually the entire downward extent of the middle region of the under side of the joint and is covered densely with thick but exceedingly short silvery gray bristles that are a continuation of a similar dense patch of microscopic bristles usually traceable on the inner side of the apex and upward of the hind femora. The plateau-like area is succeeded posteriorly by a sharply contrasted and abruptly flattened area (of variable width from species to species) that extends nearly from the base to the apex of the inner face of the joint and is much wider towards the apex than towards the base. The hind metatarsi of variable width from species to species as compared with the width of the hind tibiae; these metatarsi as a rule approximately straight along their anterior margin and slightly convex along their posterior margin; the sides converge a little at the base; the outer face of the joint is sometimes a little thickened anteriorly; the apex posteriorly is either rectangular to rounded or with a somewhat acute angulation. The hairs of the hind coxae¹ (reversing the condition usual in the worker) are in most species longer on the posterior face than on the anterior face. The other hairs of the leg similar in distribution and character to those of the worker but on the whole not quite so abundant. Those on the under side of the trochanters often shorter than in the conspecific worker. The hairs of the femora, as in the worker, fewer and shorter than those of the tibiae (especially is this true of the hairs of the fore and middle femora, those of the hind femora being sometimes more developed). The hairs particularly of the fore and middle tibiae and of all the metatarsi longer along the posterior lateral contour of the joint than along the anterior lateral contour. The hairs of the inner face of the middle tibiae usually longer (especially towards the apex) than

available, it would be found that in this instance, too, the relationship of size as between the thorax of the male and that of the worker holds. The contrast of size is greatest in *fulviventrís* and its variety *guianae*, where the thoracic length of the male exceeds that of the worker by about one-fifth. In the other species the difference is slighter. Owing to the fact that in the case of some forms the male is not known, the generalization here made is of limited application.

¹ The hairs of the hind coxae are longer posteriorly than anteriorly in the males of *pallida*, *chanchamayoënsis*, *amapana*, *williana*, *recurva*, *nigerrima*, *fulviventrís*, and *compressa*. On the other hand, if the limited number of males before me are representative, then at least in typical *trinidadensis*, in *hyalinata* variety *branneri*, and in *ruficrus* the hairs on the anterior face of the hind coxae of the males of these forms tend to be longer seemingly than the hairs along the posterior face of this joint.

the hairs of the outer face, and the hairs of this outer face (as in the worker) usually longer than the hairs of the outer face of the fore tibiae, although the hairs of the outer face of both fore and middle tibiae are in some species distinctly short. The intermixed plumose hairs that are usual on the outer face of the middle tibiae of the worker are as a rule also present in the male, although sometimes less abundant than in the conspecific worker, and the plumose fringing hairs along the posterior contour of the hind tibiae of the worker appear as a rule also in this area of the male. The hairs on the outer face of the fore and middle metatarsi and posteriorly on these joints distinctly longer than the hairs of the metatarsal brushes of the fore and middle legs. The inner face of the hind metatarsi with a suboval, sericeous, silvery gray patch at the base that, because of the flattened character of its hairs, stands more or less in sharp contrast to the bristle-covered apical part of the joint (but the contrast is sometimes less marked than in the conspecific worker). Small joints of tarsi moderately hairy; claws cleft with a well-developed pulvillus.

WINGS: As described for the worker. Number of hamuli in the relatively limited representation of males available for study ranges from four to six, but the failure of these males to show a greater maximum in the case of species (like *trinidadensis*) where the worker may have as many as eight hamuli is probably owing to the paucity of the male specimens, as eight hamuli are a rarity even among the abundant workers of such species.

ABDOMEN: Usually a little more elongate than that of the conspecific worker; its ventral surface rarely trigonate, usually somewhat flattened down the middle of the sternites, especially in the case of those sternites near the apex of the abdomen; the tergites usually gently arched as are those of the worker, but in one instance (*compressa*) laterally compressed and ridged dorsally. The chitin smooth and sculptureless or virtually sculptureless. Tergite 1, and in some cases also tergite 2, bare, but usually there is a narrow band of inconspicuous hairs (as a rule appressed) along the apex of tergite 2 and ex-

tending also sometimes up the sides of that tergite. The apex also of tergite 3 usually only inconspicuously covered with hair, but the apex of the subsequent tergites usually with longer erect hairs. Tergite 1 with a crescentic depression along its apex (sometimes a little difficult to trace, particularly in species of small stature), and tergite 2 also depressed along its apex, although the depression is usually more shallow than that of tergite 1. The ventral aspect of the abdomen usually without or virtually without the erect hairs down its middle that are present in the corresponding area of the worker; instead, the under side of the abdomen of the male is covered on the apical half of the sternites, especially on sternites 3 to 5, densely with appressed sericeous hairs, which often present a continuous array due to the telescoping of these sternites. Sternite 6 with a median spine at the apex, which is more fully revealed in dissection.

DISCUSSION

The subgenus *Trigona* is of all the Meliponidae the one seemingly best equipped structurally, and with the subgenus *Tetragona* belongs in my estimation at the top of the family tree. In common with the worker of *Tetragona* the worker of subgenus *Trigona* and, as a rule, also its male have plumose hairs fringing the hind tibiae, but the worker of *Trigona* can readily be distinguished from the worker of the subgenus *Tetragona* by the completely toothed apex of its mandible, which in most species of *Trigona* is quinque-dentate, more rarely quadridentate. Only the worker of the subgenus *Paratrigona* among the Meliponidae approaches that of *Trigona* in having a completely dentate mandible, but in *Paratrigona* the number of teeth is always limited to four. Not only are there plumose hairs fringing the hind tibiae of the worker and frequently of the male of subgenus *Trigona*; such hairs are usual also on the outer face of the middle tibiae of these castes. Hairs of this character are excellent working tools, of service in the retention of any material with which the hind legs are loaded. It should be noted that these plumose hairs usually have the feathery fringe confined to the upper surface only of the hair,

the lower surface being in the vast preponderance of instances simple.

Alone among the social bees, male stingless bees, it is said, assist in the construction of the nest. According to my examination of specimens of that sex under the microscope, it is males of the subgenus *Trigona* that in a few instances have had adhesive material on the hind tibiae, and it may be that participation on the part of the male in nest activities, if it indeed occurs (and the if is a big IF), is confined to those subgenera in which the male is structurally more fitted for the task. In many males of the subgenus *Trigona* the hind tibiae of the male resemble the hind tibiae of the worker rather more than the hind tibiae of the queen resemble those of the worker and seem, therefore, somewhat adapted for tasks not dissimilar to those performed by the hind tibiae of the worker. The presence, above referred to, of adhesive material on these hind tibiae might accordingly seem to clinch the argument in favor of the industry of the male, but it is also possible that the adhesive material was accidentally acquired by the males in question by blundering against a sticky surface, and that even males of the subgenus *Trigona* should only doubtfully be included among the constructive individuals of the colony. The attribution of industry to the male seems to derive from the claim that the male like the worker is a wax producer, a claim that is still in need of substantiation. The fact that such useful functions as have been ascribed to male stingless bees are without parallel among Apoidea should make for caution in accepting them as established facts. The reader is referred to the Introduction (p. 44) for a fuller discussion of this subject.

An interesting structural character to be noted in the subgenus *Trigona* is the differentiated area at the base of the inner face of the hind metatarsi, where appressed sericeous hairs occupy an oval space that is in sharp contrast with the erect bristles of the metatarsal brush over the rest of the inner face of the joint. This character occurs not only in all the workers but also in all the males of subgenus *Trigona* and, so far as the New World is concerned, is almost their passport of identification, being shared, out-

side of this subgenus, only by a very few species of *Tetragona*¹ and, so far as known, only in the worker of these species. But in the Indo-Malayan region it is usual for members of the subgenus *Tetragona* to evidence this distinctive character of *Trigona*, and the character is, therefore, less reliable for the division of these two closely related subgenera than a study of the New World species exclusively might lead one to hope is the case.

Members of the subgenus *Trigona* show considerable adaptability in the selection of nest sites, and even within a given species the behavior is often by no means stereotyped (see discussion of *amalihea*). Many nests are built in the open, others in hollows within trees or walls. While some nests are securely lodged in the interior of a termite structure or even a formicary, others have merely the limited protection of a bromeliad. In contrast to arboreal nests, which are the predominant form, some nests may be subterranean (*recurva*, *fulviventr*), even in species (*fulviventr*) that usually build above ground. As a rule the nests have the brood cells arranged in horizontally placed combs after the usual manner in Meliponidae, but sometimes the combs are arranged spirally (*amalihea*, *ruficrus*), an arrangement which is not confined, however, to the subgenus *Trigona*. The entrance hole is usually made conspicuous by an externally projecting tube or trumpet, but some nests lack such architectural features.

Certain nests attain a great size, and others have attained not only size but also an impressive age. Salt (1929, p. 439) recorded a nest of *amalihea* that had 35 tiers of cells (at least 20,000 cells), while Nevermann wrote me regarding a nest of *corvina* which was 10 years old.

Members of this subgenus are often very aggressive (*amalihea*, *ruficrus*, *trinidadensis*), while others (*fulviventr*) are timid. Several of the species (*amalihea*, *trinidadensis*, *trinidadensis* variety *silvestriana*, *ruficrus*, *corvina*, *nigerrima*) are destructive of fruit trees, notably *Citrus*. Several species share with members of the subgenus *Oxytrigona* a par-

¹ *Jaty* F. Smith, *jaty* variety *febrigi* Schwarz, *pfeifferi* Friese, *buchwaldi* Friese, *buchwaldi* variety *weyrauchi* Schwarz.

tiality for the secretions of membracids. On the whole the bees of the subgenus *Trigona* are a group of unclean habits; they are frequently taken on excrement, which they use as building material in their nests, as well as on dead animals, but in common with other bees they are also visitors of flowers.

KEYS TO THE SPECIES AND VARIETIES OF
Trigona (*Trigona*)

WORKERS

(Exclusive of *pallida* variety *muzoënsis*, new variety, worker of which is unknown, of *amapana*, new species, known only from the male, and of *braueri* Friese, of which I have not seen a specimen.)

1. The mandibles quinquedentate, although the two innermost teeth are sometimes very small; the teeth usually distinctly separated but occasionally with thin intervening septa of chitin 2
The mandibles with three usually distinct teeth along the outer half or two-thirds of the apex of the mandible, although the dentition is sometimes interrupted by a thin septum of chitin between the first two teeth; a fourth tooth or merely an angle at the inner end of the apex of the mandible. The outer face of the third tibiae rather decidedly excavated near the apex 21
2. The color of the head, the thorax, and the abdomen black or at least deep brown or fuscous. The legs usually mainly black or deep brown but sometimes with yellow or ferruginous hind tibiae 3
The head, thorax, or abdomen (usually all of these parts) extensively or exclusively ferruginous or fulvous; the legs almost invariably ferruginous or tawny, with no or very little black 17
3. The basal half of the wing of iodine stain, the sharply contrasted apical half milky white owing to the presence of microscopic pale hairs; the stigma and veins of the apical half bright ferruginous. The clypeus wide, its greatest width about three times that of its length. Medium-sized to very large *Trigona*, with a forewing length including tegula, of about 8.5 to 10.75 mm. . . . 4
The wing, even when the base is darker than the apex, without such sharp contrasts . . 5
4. The lower half of the supraclypeus glabrous and polished; the mandibles usually predominantly reddish brown except for the black apical teeth; larger (7.5 to 10 mm.)

and especially distinguished by the great length of the wings, the forewing including tegula, measuring about 10.5 to 10.75 mm.

. . . *dimidiata* variety *dimidiata* F. Smith
The half of the supraclypeus below the antennal sockets more or less hairy like the half extending above the antennal sockets; the mandibles mainly black, with a reddish brown stripe, however, immediately behind the black apical teeth. Smaller (6 to 7.5 mm.) and with shorter wings, the forewing, including tegula, about 8.5 mm. long
. . . *dimidiata* variety *venezuelana*, new variety

5. Hind tibiae rounded along their entire apical contour, being neither emarginate nor truncate at the tip, with the result that the entire joint is without, or virtually without, angulation and of rather even contour, a little resembling in outline a baseball bat. These tibiae relatively narrow, only a little wider at the apex than are the metatarsi at the apex, and flat rather than depressed posteriorly at the apex of their outer face. The spines along the apex of the raised area on the under side of the hind tibiae short, not visible when the leg is viewed level from the outside. The clypeus flat 6
Hind tibiae of different contour and wider. Clypeus in some species flat, in others more or less raised 7
6. Relatively small: width of head about 2 mm.; width of thorax about 1.75 to 2 mm.; length of forewing, including tegula, about 5.75 mm. . . *hypogaea* variety *hypogaea* Silvestri
Relatively large: width of head about 2.5 mm.; width of thorax about 2.25 mm.; length of forewing, including tegula, about 6.75 mm.
. *hypogaea* variety *robustior* Schwarz
7. Hind tibiae very wide at the apex and rather decidedly truncate to subtruncate along the apical margin. The scutellum semicircular posteriorly. Erect black hairs on apical half of clypeus much longer than those on scape. The wings rather strongly smoky. Length of forewing, including tegula, 8 to 8.5 mm.
. *nigerrima* Cresson
The apex of the hind tibiae slightly emarginate, with at least a slight angulation where the posterior contour and the apical contour meet 8
8. Large, robust *Trigona* (specimens with retracted abdomen sometimes only 6.5 mm. but usually from 7 to 11 mm. in length; thoracic width 2.5 to 4 mm.). The clypeus foveate apically but not medianly grooved for most of its length although in rare instances faintly incised. Strongly smoky

- wings (9 to 11 mm. in length, including tegula) that extend far beyond tip of abdomen, being considerably longer than the entire body length. The angle at the apical termination of the convex posterior lateral contour of the hind tibiae distinct, sub-tooth-like to tooth-like 9
- Bees of smaller size, rarely attaining as much as 7.5 mm. in length, usually much shorter, with a wing length that even in extreme cases does not attain 9 mm. Combination of characters different from those noted for 9 10
9. The clypeus with erect black hairs, even though these are sometimes very few; the scape with similar short black hairs; the front with longer coarse black hairs of irregular growth (best noted when the insect is viewed from the side). Length of forewing, including tegula, 9.5 to 11 mm. *trinidadensis* variety *trinidadensis* Provancher
- The clypeus without erect black hairs; the scape with merely fine, down-like, inconspicuous hairs; the front with microscopic hairs of very even growth and uniform length, so minute that they are easily overlooked even when the insect is viewed from the side. Length of forewing, including tegula, about 9 to 9.5 mm. *trinidadensis* variety *silvestriana* Vachal
10. The clypeus rising only barely above the sides of the face and distinctly flattened or approximating a flattened condition (comparable with the condition of the species grouped under 6). The mandibles in the majority of cases black from base to apex except for a narrow area of red immediately behind the black apical teeth, but sometimes red. Small bees, with a forewing length, including tegula, usually 6 to 6.25 mm. (very exceptionally 5.25 mm.; see discussion of *amalihea*, p. 218) 11
- The clypeus not virtually level with the sides of the face, at least gently arched or with a median longitudinal depression. The mandibles red or brown except for the black apical teeth 12
11. The scape with distinct rather coarse to bristle-like black hairs that are comparable in length with the width of the scape and sometimes (particularly those towards the base) even longer than the scape is wide. Similar black bristles moderately abundant among the silvery gray appressed hairs of the clypeus. The whole wing rather transparent, the median and marginal cells barely, if at all, darker than the other cells.
- A small and dainty species (about 4.25 to 5.75 mm. in length), with narrow thorax (about 1.75 mm. in width). Length of forewing, including tegula, about 6 mm. *recurva* F. Smith
- The scape with very fine inconspicuous hairs that are much shorter than the scape is wide. The wings somewhat smoky especially in the median and marginal cells. Almost always larger and more robust, very exceptionally with a thorax as narrow as 1.5 mm., more usually 2 to 2.25 mm. in width. Length of forewing, including tegula, 6 to 6.25 mm. *amalihea* Olivier
12. The clypeus, on the whole, of smooth even surface, usually very gently and continuously arched, without a furrow down the middle although occasionally a little flattened or subdepressed in this region, not foveate or barely subfoveate at the middle of the apex 13
- The clypeus with a more or less developed median longitudinal channeling on depression, with the result that the region on each side of the middle seems slightly swollen. 16
13. The wings for the most part or wholly hyaline, or whitish transparent and milky. Length of bee 5 to 6.5 mm.; length of forewing, including tegula, 7.25 to 7.5 mm. 14
- The wings more or less stained in the apical as well as the basal region 15
14. The wings of a rather uniform whitish transparency throughout, and usually distinctly milky. The median cell no darker, or virtually no darker, than the other cells. The venation and stigma bright ferruginous throughout
- . . . *hyalinata* variety *hyalinata* Lepeletier
- The wings with at least the median cell more or less darkened and with the costal and subcostal veins fuscous, as well as often the veins enclosing the median cell. The cells apical of the median cell clear to slightly milky. *hyalinata* variety *branneri* Cockerell
15. The wings of a uniform, rather dull yellowish stain, of no deeper or scarcely deeper tinge in the median cell than in the cells more apically located. The venation and stigma ferruginous. Length of bee 6.25 to 7.5 mm.; length of forewing, including tegula, about 7.75 to 8 mm.
- . . . *hyalinata* variety *amazonensis* Ducke
- The wings a little smoky, with the median cell somewhat more deeply stained than those apical of it. At least a faint evidence of depression or flattening along the middle of the clypeus. Length of bee 4.75 to 5.5 mm.; length of forewing, including tegula, usually

- 6.75 to about 7.25 mm.
 *corvina* Cockerell (see also 16)
16. The black erect hairs on the clypeus (seen only when the insect is viewed from the side) rather dense and relatively long, as a rule exceeding in length the erect black hairs on the scape. The median longitudinal depression on the clypeus relatively deep. The hind tibiae and hind metatarsi in the great majority of instances ferruginous to yellowish (if black, variety *concolor* Grubod). Slightly larger: length 5.5 to 6.5 mm.; length of forewing, including tegula, about 7.5 to 7.75 mm. . . *ruficrus* Latreille
- The dark erect hairs on the clypeus fine, sparse, scattered, and sometimes even absent, less conspicuous than the appressed pale hairs of the clypeus and of shorter length than the erect black hairs on the scape, which tend to be subequal in length to the width of the scape. The median longitudinal depression on the clypeus relatively shallow, sometimes barely traceable. The hind tibiae usually black although ferruginous in callow specimens. Somewhat smaller: length 4.75 to 5.5 mm.; length of forewing, including tegula, usually about 7.25 mm. . . *corvina* Cockerell (see also 15)
17. The clypeus distinctly short and flat, rather less than one-third as long as its greatest width. The labrum obtusely triangular to rounded. Length 7 to 9 mm.; length of forewing, including tegula, 7.25 to 8 mm.
 *dallatorreana* Friese
- The clypeus relatively long, about one-half as long as its greatest width measured from one of the anterolateral extremities to the other. The labrum exceedingly faintly to rather distinctly bituberculate.18
18. Rather large bees, 6.5 to 9 mm. in length; length of forewing, including tegula, 9 to 9.5 mm. The clypeus, scape in front, and labrum light ferruginous in contrast to the darkened front and sides of face. The labrum barely elevated on each side of its middle *williana* Friese
- Much smaller bees, 4.5 to 6 mm. in length; length of forewing, including tegula, about 6 to 6.75 mm. The labrum somewhat more distinctly bituberculate19
19. The head and thorax unstained ferruginous to honey colored except for black on the teeth of the mandibles, the scape posteriorly at the apex, the flagellum more or less above, eyes more or less mottled (green in life) *pallida* variety *pallida* Latreille
- The thorax and sometimes the head more or less extensively blackened.20
20. The head unstained except for the very limited dark markings indicated for *pallida* variety *pallida* (and some of these not always present) and in addition occasionally with two or three cloudy dots above the summit of the eye that sometimes coalesce; but the thorax with a variable amount of black on the mesonotum (sometimes virtually the entire mesonotum is black; in other cases the middle area is ferruginous and the black is limited to a long cuneiform mark on each side of it; and finally there are conditions intermediate between these two extremes); sometimes a circular black spot on mesopleura. The hind metatarsi produced backward and slightly downward at their apex posteriorly so that the posterior apical angle is rather sharply acute. Length of forewing, including tegula, about 6.75 mm. . . *chanchamayoensis*, new species
- The head black except for the ferruginous clypeus, supraclypeus, lower corners of face, lower half of genal area, labrum, mandibles exclusive of teeth, scape, and flagellum below. The mesonotum black. The mesopleura with a black maculation. The hind metatarsi not produced backward or downward at their apex posteriorly; the posterior apical angle approximately rectangular. Length of forewing, including tegula, 6.5 to 6.75 mm.
 *pallida* variety *ferricauda* Cockerell
21. The labrum simple, not bituberculate. The emargination between the third tooth of the mandible and the inner extremity of the apex of the mandible very shallow, with the result that there is usually an angle rather than a tooth at this inner extremity. The black hairs on the clypeus comparable in length to those of the scape, not notably longer. The wings (forewing, including tegula, about 6.25 mm. long) usually somewhat milky in appearance except the median cell, which is apt to be somewhat darker owing to the presence of minute blackish hairs. The abdomen laterally compressed, longitudinally carinate on the dorsal side, with a more or less precipitous, gable-like, downward slant of the tergites on each side of the carina; the shape of the abdomen roughly quadrangular, subcylindrical, in rare cases even somewhat perpendicularly flattened, depending upon the degree of the lateral compression; the abdomen always much narrower than the thorax
 *compressa* Latreille
- The labrum slightly bituberculate. The emargination between the third tooth of the

mandible and the inner extremity of the apex of the mandible usually rather well defined, with a resulting quadridentate condition of the mandible, but the innermost tooth less distinct than the three outer ones. The hairs on the clypeus considerably longer than those on the scape. Length of forewing 6.5 to 7.5 mm. The wings usually of a rather uniform, slightly yellowish stain, not milky. The abdomen not laterally compressed, not ridged dorsally, not much narrower than the thorax 22

22. Abdomen fulvous to reddish.
 . . . *fulviventris* variety *fulviventris* Guérin
 Abdomen black or blackish
 . . . *fulviventris* variety *guianae* Cockerell

QUEENS

(Several of the queens in the subgenus *Trigona* are unknown and others have been so briefly described that, in the absence of the actual specimen, it might be misleading to attempt to interpret their place in the key.)

1. The head, thorax (at least for the most part), and abdomen ferruginous to fulvous. The labrum with two well-defined tubercles. The malar space measured from the lower extremity of the eye to the middle of the base of the mandible somewhat longer than the flagellum is wide. Clypeus and front largely or wholly devoid of erect hairs. The clypeus measured from one apico-lateral extremity to the other about twice as wide as long. The hind metatarsus not tapering to the apex, which is fringed with a row of spine-like hairs. The wings of a diluted yellowish gray stain 2
 The head, thorax, and abdomen predominantly dark 3
2. The mesonotum ferruginous like the rest of the thorax. The mesopleura immaculate. The hind metatarsus subrectangular posteriorly at the apex
 *pallida* variety *pallida* Latreille
 The mesonotum mostly dark brownish to blackish with a bordering ferruginous stripe on each side. The mesopleura on their lower half with a black spot anteriorly. The hind metatarsus ending in an acute angle posteriorly at the apex
 *chanchamayoensis*, new species
3. The hairs rather uniformly short, sericeous, and soft over virtually the entire head, thorax, legs, and abdomen, only the mandibles below, the scutellum, and the thorax below having hairs that are irregularly longer and somewhat coarser; the appearance somewhat velvety to silky

. *amalthaea* Olivier
 The hairs coarse and of irregular growth, more especially on the head, thorax, or legs . . 4

4. The hairs on the outer face of the hind tibiae and along the posterior lateral contour of this joint exceedingly long, for the most part not shorter, in some cases longer, than the greatest width of the hind metatarsus. The hairs of the clypeus and supraclypeus, mandibles below, mesonotum, mesopleura, and outer face of middle tibiae and middle metatarsi likewise notably long
 *nigerrima* Cresson
 The hairs on the outer face of the hind tibiae and along the posterior lateral contour of this joint not nearly so long, shorter than the hind metatarsus is wide 5
5. Malar space a little the longer, about twice as long, measured from the lower extremity of the eye to the middle of the base of the mandible, as the flagellum is wide. The hairs of the head and thorax predominantly fulvous, those on the lower part of clypeus somewhat longer than the scape is wide *trinidensis* variety *trinidensis* Provancher
 Malar space a little the shorter, about one and one-half times as long as the flagellum is wide. The hairs of the head and thorax predominantly black, those on the clypeus about as long as the scape is wide. . . . 6
6. Outer face of hind tibiae predominantly fulvous *ruficrus* Latreille
 Outer face of hind tibiae darkened at least on its posterior half . . . *corvina* Cockerell

MALES

(The males of several forms are unknown.)

1. The head and thorax largely or wholly black, blackish, or very dark brown 2
 The head and thorax wholly, or to a substantial extent, fulvous or ferruginous . . . 12
2. The clypeus and supraclypeus, as well as the mandibles, labrum, malar space, and scape at least in front ferruginous or honey colored in contrast with the dark upper half of head, sides of face, genal area, and for most part flagellum. Hairs of clypeus silvery gray. Facial quadrangle narrow, its maximum width near the summit of the eyes about six-tenths of the width of the head. Mandibles narrow at the apex, only about one-half their width at the base. Hind tibiae about the same width as their metatarsi, flattened to slightly concave (towards the apex) on their external face. Wings subhyaline, venation and stigma fuscous; length of forewing, including tegula, about

- 6 mm. 3
pallida variety *mucoensis*, new variety
 Not having the above combination of characters. Clypeus black or at least dark brown 3
3. The lateral ocelli relatively close to the compound eyes, separated from them by only a little more than the diameter of an ocellus. Facial quadrangle narrow, its maximum width near the summit of the eyes about six-elevenths of the width of the head. Hind tibiae rather narrow, only a very little wider than their metatarsi. Wings of a rather uniform diluted yellow stain, with ferruginous venation and stigma; length of forewing, including tegula, about 6.5 mm. 4
 The lateral ocelli distant from the compound eye by two to three times their own diameter 5
4. The abdomen fulvous to ferruginous
 . . . *fulviventris* variety *fulviventris* Guérin
 The abdomen black or blackish
 . . . *fulviventris* variety *guianae* Cockerell
5. The abdomen much narrower than the thorax, laterally compressed, longitudinally carinate on the dorsal side, with a more or less gable-like downward slant of the tergites on each side of the carina. The wings sometimes with more or less staining in the median cell,¹ but otherwise for the most part milky white, with ferruginous stigma and, with the exception sometimes of the slightly fuscous costal and subcostal veins, ferruginous neuration; length of forewing, including tegula, about 6 to 6.25 mm.
 *compressa* Latreille
 The tergites of the abdomen evenly arched, without a carina resulting from lateral compression 6
6. Large bees; the forewing, including tegula, 10.5 to 10.75 mm. long and more or less smoky. The mandible usually with some evidence of dentition. The malar space well defined, about as long at its middle as the median joints of the tapering flagellum are wide. Erect black hairs of head of rather uneven length *trinidadensis* variety *trinidadensis* Provancher
 Bees of shorter wing length. Mandible with no, or usually only very obscure, evidences of dentition. The malar space obsolete to obsolescent, or, at any rate, not so long at its middle as the median joints of the flagellum are wide 7
7. The clypeus with a faint median longitudinal fossa. The hind tibiae and metatarsi usually fulvous to ferruginous, strongly contrasting with their dark femora and with the dark fore legs and middle legs. Length of rather smoky forewing, including tegula, about 7.5 mm. *ruficornis* Latreille
 The clypeus not depressed down its middle, at most slightly foveate apically. The hind tibiae and metatarsi sometimes not so dark as the fore and middle legs but as a rule more or less concolorous with them 8
8. The scape devoid or virtually devoid of black hairs, or at least the minute erect silvery gray hairs far denser and more conspicuous than the black. The malar space obsolete, the inner angle of the base of the mandible grazing the rim of the eye. Length of smoky forewing, including tegula, about 6 mm. *amalthaea* Olivier
 The scape with black erect hairs; silvery gray hairs of scape, if present, appressed and less conspicuous than the black. The inner angle of the base of the mandible separated, even if sometimes very narrowly, from the rim of the eye 9
9. The wings mostly subhyaline to hyaline, with the median cell usually a trifle darker; length of forewing, including tegula, 6 to 7.25 mm. 10
 The wings more or less smoky 11
10. A little the larger. Length of forewing, including tegula, about 7.25 mm. The hind metatarsi about three-fourths the width of their rather broad tibiae and rounded posteriorly at the apex. The spine at the middle of sternite 6 (fig. 20c) narrow basally as well as apically.
 . . . *hyalinata* variety *branneri* Cockerell
 A little the smaller. Length of forewing, including tegula, about 6 mm. The hind metatarsi almost as wide as their rather narrow tibiae and somewhat angulate posteriorly at the apex. The spine at the middle of sternite 6 (fig. 15c) nearly as wide at the base as it is long. *recurva* F. Smith
11. The malar space almost obsolete, the inner angle of the base of the mandible very nearly in contact with the rim of the eye. The erect black hairs on the clypeus short, not so long as the scape is wide. Length of forewing, including tegula, about 6.75 mm. to 7 mm. *corvina* Cockerell

¹ Ducke (1925, p. 388) had specimens of *compressa* that approximated the wing coloration of *dimidiata*. The male of *dimidiata* is unknown and hence is not included in this key. In the worker the basal half of the wing is of iodine stain and sharply contrasts with the milky apical half, and it is to be presumed that the wing of the unknown male of *dimidiata* and of *dimidiata* variety *venezuelana* is similarly characterized.

The malar space more developed, eye and base of mandible distinctly separated. The erect black hairs on the clypeus long, considerably longer than the scape is wide. Length of rather dark forewing, including tegula, about 8 mm. . . . *nigerrima* Cresson

12. The genal area wider than the eye. The clypeus twice as wide as it is long. The relatively wide face rather densely covered with long coarse fulvous hairs, those on the scape nearly as long as the scape is wide. Malar space fairly distinct. Hind tibiae about twice as wide as their metatarsi and with only erect hairs (and those few and simple) over their outer face, contrasting with the dense fringe of pale plumose hairs along the posterior contour of these tibiae. Length of forewing, including tegula, about 7 mm. *dallatorreana* Friese

The eye distinctly wider than the genal area. The clypeus less than twice as wide as long. The face more moderately hirsute. The inner angle of the base of the mandible grazing or almost grazing the eye. The hind metatarsi at least three-fourths as wide as the hind tibiae; the hind tibiae rather densely covered over their outer face with semi-erect simple hairs in addition to sometimes abundant appressed feathery hairs. 13

13. Large bees, about 8 mm. in length; length of forewing, including tegula, about 8.5 to 9 mm. Face exceedingly narrow. The clypeus relatively long, its length slightly more than two-thirds its greatest width. The ocelli large, the lateral ones separated from the nearest compound eye each by about its own diameter. The hind metatarsi three-fourths as wide as the hind tibiae; the outer face of the hind tibiae with usually many feathery hairs *williana* Friese
Smaller bees, about 5 to 5.5 mm.; length of forewing, including tegula, 5.75 to 6.75 mm. 14

14. The face narrow; the ocelli rather large, each lateral ocellus separated from the nearest compound eye by only about its own diameter *amapana*, new species
The face somewhat wider; the ocelli small, each lateral ocellus separated from the nearest compound eye by at least twice its own diameter 15

15. The head and mesonotum ferruginous *pallida* variety *pallida* Latreille
The head predominantly ferruginous but sometimes with a down-pointing dark triangle between the ocelli and the top of the supraclypeus. The mesonotum either with a large black cuneiform maculation on each

side of an otherwise ferruginous surface or black throughout except for narrow ferruginous side and hind margins
. *chanchamayoensis*, new species

Trigona (*Trigona*) *amalthaea* (Olivier)

- Apis Amalthaea* OLIVIER, 1789, pp. 78-79.
Apis amalthaea, FABRICIUS, 1793, pp. 325-326.
Apis amalthaea, LATREILLE, 1802a, p. 386.
Apis amalthaea, LATREILLE, 1802b, p. 438.
Apis amalthaea, TIGNY, 1802, pp. 74-76.
Apis amalthaea, LATREILLE, 1803, pp. 48-49.
Apis amalthaea, FABRICIUS, 1804, p. 371.
Apis amalthaea, LATREILLE, 1804a, p. 393.
Apis amalthaea, LATREILLE, 1804b, pp. 174-175, pl. 13, fig. 13.
Apis amalthaea, LATREILLE, 1805, p. 68.
Melipona Amalthaea, ILLIGER, 1806, p. 156.
Trigona Amalthaea, JURINE, 1807, p. 246 (misprinted 146).
Trigona amalthaea, LATREILLE, 1809, p. 183.
? "Amalthée," WALCKENAER, in Azara, 1809, pp. 165-166.
? *Trigona amalthaea*, LATREILLE, "1811"b, p. 294.
Trigona Amalthaea, KIRBY AND SPENCE, 1815, pp. 319-320.
Apis amalthaea, DUMERIL, 1816, pp. 63-64.
Melipona Amalthaea, LAMARCK, 1817, p. 52.
"L'abeille Amalthée," LATREILLE, 1818, pp. 85-86.
"L'abeille amalthée," DUMERIL, 1823, p. 534.
"L'abeille amalthée," DUMERIL, 1824, p. 49.
Trigona Amalthaea, LEPELETIER, 1825, p. 710.
Melipona amalthaea, BOITARD, 1828, p. 289.
? "Sanharo miudo," SPIX AND MARTIUS, 1828, p. 542.
Trigona Amalthaea, PERTY, [1833], p. 26.
Melipona Amalthaea, PERTY, [1833], p. 27.
Melipona Amalthaea, LAMARCK, 1835, p. 272.
Melipona (*Trigona*) *amalthaea*, LEPELETIER, 1836, pp. 425-426. The description of the nest, virtually a transcript of the description given by Olivier, applies to *amalthaea*, but the description of the insect is based probably on *trinidensis*.
? *Trigona Amalthaea*, HALIDAY, 1837, p. 321 (read 1834).
? *Trigona amalthaea*, SAY, 1837, p. 415.
Trigona amalthaea, BLANCHARD, 1840, p. 403.
Trigona amalthaea, WESTWOOD, 1840, p. 286.
Melipona Amalthaea, BOITARD, 1843, p. 205.
Trigona amalthaea, DRAPIER, 1845, p. 511.
? "*Trigona Amalthée*," GOUDOT, 1846, p. 713.
Trigona amalthaea, BLANCHARD, 1849b, p. 668.
Trigona Amalthaea, BURMEISTER, 1853, pp. 219-220.
? *Trigona amalthaea*, JARDINE, 1859, p. 292, pl. 27, fig. 1.
? *Trigona amalthaea*, SAY, 1859, p. 788.

- Trigona amalihea*, F. SMITH, 1863a, p. 510, pl. 20, fig. 13.
Trigona Amalihea, GIRARD, 1879, pp. 724-725.
 ? *Trigona Amalihea*, GRONEN, 1881b, p. 332.
 ? *Trigona Amalihea*, GRONEN, 1881c, pp. 110-113.
Melipona amalihea, DALLA TORRE, 1896, p. 574.
Trigona fuscipennis FRIESE, 1900a, p. 385.
Melipona ruficrus, DUCKE, 1901, pp. 29, 51, 64.
Melipona fuscipennis, DUCKE, 1902a, pp. 325, 326, 419.
Melipona (Trigona) fuscipennis, DUCKE, 1902b, pp. 292, 314.
Trigona fuscipennis, SILVESTRI, 1902a, p. 25.
Trigona fuscipennis, SILVESTRI, 1902b, pp. 138-139.
Melipona fuscipennis, SILVESTRI, 1903, pp. 187, 212.
Trigona fuscipennis, BUTTEL-REEPEN, 1903a, p. 133.
 ? *Trigona friesei* H. VON IHERING, 1903, p. 204.
Trigona friesei, SCHULZ, 1904b, p. 827.
Trigona fuscipennis, H. VON IHERING, 1904b, p. 386.
Trigona fuscipennis, DUCKE, 1907, p. 89.
Trigona fuscipennis, DUCKE, 1908b, p. 80.
Trigona amalihea, VACHAL, 1908, pp. 221-222.
Trigona amalihea, BURMEISTER, in Friese, 1909a, pp. 35-36. (A transcript from Burmeister in an article by Friese.)
Trigona amalihea, DUCKE, 1910a, p. 108.
Trigona fuscipennis, BERTONI, 1911, p. 142.
Trigona amalihea, MARIANNO, 1911, pp. 7, 13, 79, 97.
 ? *Trigona friesei*, H. VON IHERING, 1912, p. 44.
Trigona amalihea, COCKERELL, 1912b, p. 60.
Trigona amalihea, COCKERELL, 1912c, p. 314.
Trigona amalihea, WHEELER, 1913, pp. 1-2 (identified by T. D. A. Cockerell).
Trigona amalihea, COCKERELL, 1913a, p. 10.
Trigona amalihea, COCKERELL, 1914b, p. 309.
Trigona amalihea, SCHROTTKY, 1914, pp. 218-219.
Trigona amalihea, COCKERELL, 1916, p. 3.
Melipona ruficrus subspecies *fuscipennis*, DUCKE, 1916, pp. 15, 131.
Trigona amalihea, BERTONI, 1918, p. 224.
 ? *Trigona fuscipennis*, STRAND, 1919, p. 69 (possibly *Trigona corvina* Cockerell).
Trigona amalihea, COCKERELL, 1920c, p. 465.
Trigona amalihea, LUTZ AND COCKERELL, 1920, p. 495.
Trigona fuscipennis, LUTZ AND COCKERELL, 1920, p. 498.
Trigona fuscipennis, HEGH, 1922, p. 593.
Trigona amalihea, LUTZ, 1924a, pp. 205, 208, 211, 212, 215, 216 (identified by T. D. A. Cockerell).
Trigona fuscipennis, LUTZ, 1924a, pp. 205, 207, 208, 216.
Melipona ruficrus subspecies *fuscipennis*, DUCKE, 1925, pp. 344, 419.
Trigona amalihea, L. E. CHEESMAN, 1929, p. 149.
Trigona amalihea, SALT, 1929, pp. 438-441, 447, 449, 455, pl. 23 (identified by H. F. Schwarz).
Trigona amalihea, BEQUAERT, 1932, p. 17 (identified by H. F. Schwarz).
Trigona amalihea, SCHWARZ, 1932a, pp. 231, 253, 255, 256.
Trigona amalihea, M. BATES, 1933, p. 47.
Trigona amalihea, RAU, 1933, pp. 16, 27, 37 (identified by H. F. Schwarz).
Trigona amalihea, SCHWARZ, 1934, pp. 3, 9.
Trigona fuscipennis, MAIDL, 1934, p. 167.
Trigona ruficrus subspecies *fuscipennis*, MAIDL, 1934, p. 572.
Trigona amalihea, MAIDL, 1934, pp. 660, 663.
Trigona (Trigona) amalihea, SCHWARZ, 1938, pp. 437, 442, 455-457.
Trigona amalihea, MOURE, 1944a, p. 73.
Trigona amalihea, BALLOU, 1945, p. 129.
Trigona (Trigona) amalihea, FLEMING, 1945, p. 267 (identified by H. F. Schwarz).
Melipona ruficrus subspecies *fuscipennis*, DUCKE, 1945, pp. 14, 99.

WORKER

DIAGNOSTIC CHARACTERS: Black. Mandible five toothed, black but almost without exception banded narrowly with red just before the apex. Length of malar space somewhat less than width of flagellum. Clypeus completely flat, its length not quite one-half its greatest width, with no, or virtually no, erect hairs. Scape also without black bristles. Hind tibiae with a feeble inwardly placed angle at apex posteriorly. Wings somewhat smoky.

HEAD: Black. The facial quadrangle wide, the distance between the compound eyes at the level just below the anterior ocellus about equal to the distance from the anterior ocellus to the apex of the clypeus. The compound eyes rather strongly convergent below, the distance that separates them at their level of greatest approximation (below) being about as 6.5 is to 8 when compared with their divergence at the level just below the anterior ocellus. The clypeus raised only barely above the level of the sides of the face, absolutely flat and even over its surface, not medianly grooved, not foveate apically. The length of the clypeus not quite one-half its

greatest width measured from one antero-lateral extremity to the other; each antero-lateral extremity separated from the nearest compound eye by distinctly less than the width of the flagellum. The labrum simple. The mandibles armed with five teeth (fig. 10). The malar space measured from the lower extremity of the eye to the base of the mandible at the middle somewhat less than the width of the flagellum. The distance between the lateral ocelli a little less than that between each lateral ocellus and the nearest compound eye. The carina behind the ocelli moderately developed and somewhat blunt. Clypeus, front, vertex, and lower one-third of genal area more or less moderately shiny. The clypeus lightly covered with silvery gray appressed microscopic hairs; the sides of the face with similar somewhat denser hairs and to a lesser extent such hairs are also on the front; the genal area silvery gray pruinose on its upper two-thirds. The erect hairs of the head sparse, exceptionally short and black or almost exclusively black. No, or virtually no, black hairs on clypeus. The scape with merely ultra-fine, microscopic, down-like inconspicuous pale hairs that are not in the least coarse or bristle-like and much shorter than the scape is wide. The lower half of the front without black hairs, and even the hairs of the upper half short and rather inconspicuous. The black hairs of the



FIG. 10. Mandible of worker of *Trigona* (*Trigona*) *amalihea* (Olivier). Drawing by Elena Feld.

vertex, lower one-third of genal area, and lower margin of mandible are of moderate length; a few paler hairs frequently towards the apex of the mandible below. The mandibles black for most of their extent but almost invariably with a vivid and sharply defined red stripe just behind the black teeth. The antennal sockets ferruginous. The scape usually entirely black, and the flagellum sometimes so but more often black above and more or less dull brownish below.

THORAX: Black, of somewhat subdued sheen, especially on the mesonotum, due to the presence of rather dull gray to more or less brownish tomentum; more or less dull gray tomentum also on pleura and sides of

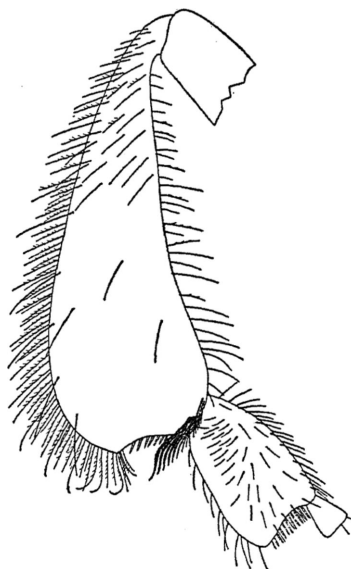


FIG. 11. Hind tibia and metatarsus of the worker of *Trigona* (*Trigona*) *amalihea* (Olivier). Drawing by Elena Feld.

propodeum in addition to the longer, more conspicuous but sparser simple black hairs in these areas and on the mesonotum and scutellum. The relative length of the thoracic hairs as indicated in the description of the subgenus *Trigona*.

LEGS: Black to frequently more or less brownish and even when the other joints are dark, the apical part of the apical joint of the tarsi tipped with ferruginous. The hind tibiae (fig. 11) clavate in outline, much wider at the apex than at the base, their anterior lateral contour gently emarginate, their posterior lateral contour strongly convex; their apex with an inconspicuous angle anteriorly that bears the comb, this followed by a bulge in the apical contour, beyond this bulge the apex is somewhat emarginate with the result that a feeble inwardly placed angle is formed where this shallow emargination of the apex encounters the posterior contour of the joint; the outer face of the hind tibiae so gently arched as to approximate a flattened condition over its basal two-thirds, and sharply

flattened to slightly excavated over approximately the apical one-third. The flattened area margining the under side of the hind tibiae posteriorly about one-third the width of the joint near the apex. The hind metatarsi about three-fifths as wide at their widest (near the apex) as the hind tibiae are wide at their widest, their posterior apical angle slightly acute to almost rectangular. The hairs of the legs predominantly black but with the following relatively minor exceptions: the short hairs on the under side of the front trochanters and the dense but very microscopic fringe on the under side of the femora (barely traceable except in the case of the middle femora) gray to whitish; the plumose hairs intermixed with the black simple hairs on the external face of the middle tibiae brownish to blackish; the microscopic but stubby hairs on the elevated part of the under side of the hind tibiae and adjacent apical part beneath of hind femora silvery gray; the suboval sericeous patch at the base of the under side of the hind metatarsi also silvery gray to whitish, but the color of its hairs often obscured by adherent foreign matter; the metatarsal brushes black to copper colored. The relative length of the hairs and their distribution as indicated in the description of the worker of the subgenus *Trigona*.

WINGS: Somewhat smoky (a little more so in the median and marginal cells) and the venation and stigma brownish to fuscous. The vestiges of the transverse cubital veins usually readily traceable, moderately defined. First discoidal cell about eight-tenths as long as the marginal cell. Number of hamuli on each lower wing usually five, sometimes six, very rarely as many as seven or as few as four. Out of 200 wings examined, 159 had five hamuli, 33 had six hamuli, four had seven hamuli, and four had four hamuli, an average of 5.19. The tegulae are black or blackish.

ABDOMEN: Black or blackish, usually telescoped and fairly compact, trigonate, comparable in width with the thorax. The hairs black. Tergites 2 and 3 with a narrow band of feeble microscopic tessellation along the apex, corresponding with the presence of the appressed hairs. A few more erect hairs usually on tergite 3, on the apical half of

tergites 4 and 5, and on tergite 6. Where these hairs emerge, the surface is sometimes somewhat granular. The venter with black erect hairs down the middle, supplemented on sternites 3 to 5 by sericeous hairs on each side that, viewed from certain angles, seem dark but from other angles silvery. The hairs of the venter seem continuous owing to the usual telescoping of the abdomen but are actually confined to approximately the apical half of the several sternites.

MEASUREMENTS: Length 4.75 to 6 mm.; width of thorax 2 to 2.25 mm.; length of forewing, including tegula, 6 to 6.25 mm. (These are the usual dimensions; for exceptions, see discussion.)

QUEEN (VIRGIN)¹

HEAD: A trifle wider than the mesonotum but considerably narrower than the distance from the outer rim of one of the tegulae to the outer rim of the other. The facial quadrangle wide, the distance between the compound eyes at their summit about equal to the distance that separates the middle ocellus from the apical margin of the clypeus. The eyes only slightly convergent below, their length approximating that of the eyes of the worker from the same locality but their width notably less. Eyes not in the least hairy. The clypeus not so uniformly or extensively flat as in the worker, its sides on their basal one-half steeply descending, with

¹ Description based on a specimen from Rio Frio, Magdalena, Colombia, collected by G. Salt on September 27, 1927. It is doubtless one of the two specimens to which Salt (1929, p. 439) refers in the phrase I have italicized:

"At the edge of the tier of brood cells; in the middle of the nest and usually attached to the comb but in one or two cases to the involucre or its supports, were found in all twenty-six cerumen pots, only very little smaller than the pollen- and honey-pots, which they resembled. These were the cells of the young females. *Two contained adult female bees*, two pupae, and the remainder full-grown larvae."

If the female on which my description is based is the same as one of these two cell-occupying young queens, it is remarkable that the insect shows (in the coloration of its chitin at least) virtually no traces of a callow state. It is possible, however, that the hairs, which are predominantly gray in this specimen, may be darker in *amalthaea* queens of greater maturity, although the coloration of the hairs of the queen tends to be lighter, when compared to the coloration of those of the worker, in the other species as well of the subgenus *Trigona* here reported upon.

the result that both the clypeus and also the elevated supraclypeus seem more protuberant than is the case in the rather flat-faced worker. The clypeus without median channeling and not foveate apically. The width of the clypeus, measured from one apico-lateral extremity to the other, is about twice its length. The labrum simple, rounded in apical contour, with an indistinct tubercle barely evident at the middle. The mandibles distinctly toothed from end to end of the apex (five teeth in all). The length of the malar space distinctly greater than the width of the scape and roughly about one-sixth as long as the eye. The ocelli small and remote from the eye, the distance from the summit of the eye to the nearest lateral ocellus being fully one and one-half times that separating the lateral ocelli from each other. The carina behind the ocelli rather distinct. The head moderately shiny, clothed rather densely with very short fine hairs (somewhat plush-like when viewed from the side) on clypeus, sides of face, front, vertex, and scape. These hairs faintly brownish in some lights, silvery grayish in others; those of the genal area more distinctly silvery gray, very dense, and for the most part more appressed. Only the hairs along the inferior margin of the mandible tend to be long (but scarcely so long as the mandible is wide at the base) and these hairs are black. Shorter, silvery gray hairs abundant over the outer face of the mandibles, which are basally black and have the apical teeth black but with a somewhat wider red area behind the apex than is usual in the mandible of the worker. Some invasion of brownish on the clypeus, but the head for the most part black or blackish to the inclusion of the scape and the flagellum, which is dark below as well as above, the scape being about one-half as long as the flagellum.

THORAX: Black to deep brownish, wider than that of the worker. The length of the mesonotum plus scutellum barely greater than the width of the mesonotum at the base. The hairs rather short, dense, sericeous, semi-erect to semi-appressed, and grayish to fuscous on the mesonotum and pleura, with longer, somewhat coarser, more or less horizontally directed blackish hairs on the scutellum. The middle area of the propodeum shiny and hairless.

LEGS: Deep reddish brown to blackish, the apical joints of the tarsi a trifle more reddish than the joints preceding. The hind tibiae a trifle longer than the combined length of the hind trochanters plus femora, somewhat clavate in outline, their apex feebly rounded anteriorly, barely angular posteriorly. The hind metatarsi at their widest are at least three-fifths as wide as the hind tibiae at their widest (near the apex) and they taper slightly downward; the length of the combined small joints of the hind tarsi about four-fifths that of the hind metatarsi measured along the inner face; the inner face covered densely from base to apex with fine, light golden bristles. Fine hairs of similar hue on the inner face of the anterior and middle metatarsi. The other hairs of the legs for the most part grayish, simple, rather uniformly short and of fine texture, sericeous, erect to semi-erect, of rather even density over most of the joints except the upper face of the trochanters and the inner (posterior) face of the femora, which are more or less glabrous. The hairs on the outer face of the tibiae only a trifle longer progressively from the fore pair to the hind pair, and those along the posterior lateral contour of the several metatarsi a trifle longer than those along the anterior lateral contour of these joints, but nevertheless distinctly short.

WINGS: Somewhat smoky (a trifle more so in the median and marginal cells) and the venation and stigma brownish to fuscous. Wings distinctly longer than in the worker, but nevertheless short when compared to the body length, for they extend only a little beyond the apex of the third tergite of the abdomen. The tegulae black. Number of hamuli per lower wing five.

ABDOMEN: Blackish. Tergite 1 smooth, with relatively sparse hairs laterally, especially towards the apex. The subsequent tergites (or at least the exposed parts of these tergites, the base being concealed) covered densely and evenly with fine, semi-erect, sericeous gray hairs that are rather uniformly short throughout except for a few longer, more erect hairs, especially on tergite 3. The exposed parts of tergites 2 to 6 densely punctate. The hairs on the apical one-half of the abdominal sternites grayish, a little more erect and a little longer than those on the

tergites but only very slightly differentiated from the latter.

MEASUREMENTS: Length about 9.5 mm. (of which the abdomen occupies about 4.5 mm.); width of thorax about 3.75 mm.; length of forewing, including tegula, about 7.75 mm.

MALE

HEAD: Black. The facial quadrangle narrower than in the worker. The distance from one eye to the other at their level of closest approximation (below) only about five-sevenths the length of the eye, whereas in the worker the distance separating one eye from the other at the corresponding level is about equal to the length of the eye. The clypeus a trifle less flat than in the worker, its apico-lateral angles grazing the rim of the eye and acute, its length a little more than one-half its greatest width. The labrum simple. The mandibles without or with only the feeblest traces of dentition along the inwardly receding apical edge; a red stripe (as in the worker) traverses the mandibles just behind this apical edge and sometimes reddens also the edge. The malar space virtually obsolete, the inner angle at the base of the mandible and the rim of the eye being in contact. The distance between the lateral ocelli definitely greater than that between each lateral ocellus and the nearest compound eye. The carina behind the ocelli moderately developed and somewhat blunt. The head a little more hirsute than that of the worker but notably less so than in the male of *trinidadensis* and *ruficrus*. In addition to the silvery gray appressed tomentum abundant on clypeus, sides of face, and front, there are a few diminutive dark hairs on the clypeus (especially on the apical half). The hairs of the scape just a degree less fine than those on the scape of the worker but shorter than those on the scape of the male of the closely related *recurva*. The black erect hairs of the front, vertex, and lower margin of mandibles similar to those of the worker. The antennal sockets ferruginous. The black scape with usually a more or less defined dull brownish to ferruginous stripe and the flagellum more or less similarly colored below.

THORAX: Black, of somewhat subdued sheen, especially on the mesonotum, owing

to the presence of grayish to darker tomentum. The erect hairs of the thorax black.

LEGS: Black, with especially the hind tibiae, however, more or less invaded by brown and the apical joint of the tarsi sometimes a little more brownish than the joints preceding. The hind tibiae very feebly concave over their anterior lateral contour and much more emphatically convex over their posterior lateral contour, the contour of their apex approximately round, their greatest width (near the apex) fully four-fifths that of the conspecific worker at the corresponding level. The hind metatarsi about three-fifths as wide at their widest (near the apex) as the hind tibiae are wide at their widest, the posterior apical angle barely acute to rounded. The hairs of the leg predominantly black or blackish with the following relatively inconspicuous exceptions: the hairs on the under side of the trochanters, the dense fringe of very microscopic hairs on the under side of the femora (more readily traceable in the case of the middle femora than in the fore or hind pair), and the appressed sericeous hairs of the oval patch on the under side of the hind metatarsi are all grayish to white; the plumose hairs intermixed with the black simple hairs on the external face, especially posteriorly, of the middle tibiae are sometimes dark grayish to brownish rather than black as are also as a rule the hairs of the posterior lateral contour of the hind tibiae; the microscopic but stubby hairs on the elevated part of the under side of the hind tibiae and adjacent apical part beneath of the hind femora are silvery gray; the metatarsal brushes black to copper colored. The mainly plumose fringe along the posterior lateral contour of the hind tibiae dense, the longer hairs usually subequal to one-half the maximum width of these tibiae. The distribution of the simple black hairs in general and their relative length approximately as indicated in the generalized description of the male of the subgenus *Trigona*.

WINGS: Somewhat smoky, like those of the worker. Number of hamuli in the 10 wings available for examination uniformly five.

ABDOMEN: Black or blackish, comparable in width with the thorax. The hairs of the tergites black: tergites 2 and 3 with a band of appressed hairs apically; tergites 4 to 6 with

the hairs longer and semi-erect; tergite 7 with an apical fringe of short hairs. The sericeous hairs of the venter silvery gray. (Fig. 12.)

MEASUREMENTS: Approximately the same as for the worker.

TYPE MATERIAL

The specimens (from French Guiana and Surinam) on which Olivier based his description are apparently no longer in existence.

ently be developed under three headings: (1) interpretations based on the early descriptions; (2) interpretations based on the biology; (3) interpretations based on the geographic distribution.

1. Interpretations based on the early descriptions. Olivier described *amalthea* in 1789 and during the succeeding quarter of a century it was noted or described twice by Fabricius (1793, pp. 325-326; 1804, p. 371),

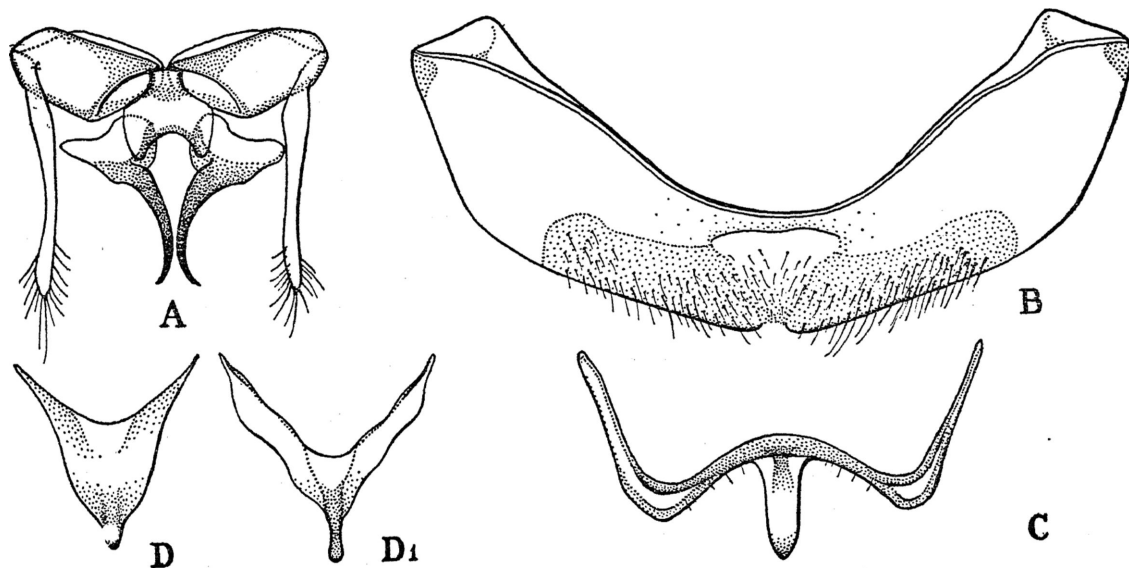


FIG. 12. Abdominal parts of the male *Trigona* (*Trigona*) *amalthea* (Olivier). A. Genitalia (chitinized parts only). B. Sternite 5. C. Sternite 6. D. Sternite 7. All based on specimens from San José, Costa Rica. D1. Sternite 7 of a specimen from Pernambuco, Brazil. Drawings by Shirley H. Risser.

DISCUSSION

The identity of Olivier's *amalthea* has long perplexed those who have studied the Meliponidae, and it is doubtful whether a decision that will have finality can be arrived at. Most investigators have identified *amalthea* either as the bee described by Friese as *fuscipennis* (a relatively small insect) or as that designated by Provancher as *trinidensis* and by Vachal as *silvestriana*¹ (a relatively large insect). This discussion may conveni-

¹ Vachal's *silvestriana*, as suspected by Friese (1917, p. 299) and also by Cockerell (1925c, pp. 626-627), is, at least in so far as Vachal's South American specimens are concerned, a synonym of Provancher's *trinidensis*, as I had a chance sometime ago of ascertaining by an examination of the type of *trinidensis* in the Public Museum in Quebec, but the type material was undoubtedly composite and the name *silvestriana* is here retained for Vachal's Central American specimens.

eight times by Latreille (1802a, p. 386; 1802b, p. 438; 1803, pp. 48-49; 1804a, p. 393; 1804b, pp. 174-175; 1805, p. 68; 1809, p. 183; "1811b," p. 294), and once each by Illiger (1806, p. 156), Tigny (1802, pp. 74-76), and Jurine (1807, p. 246). Moreover drawings of it were made by Coquebert (1804, pl. 22, fig. 4) and by Meunier (Latreille, 1804b, pl. 13, fig. 13). It might seem as though such a wealth of evidence would leave no room for doubt, but not only is the evidence conflicting as between the two artists, but even in Olivier's description itself, which one would like to rely upon as a finality, some characters fit *fuscipennis* while others fit *trinidensis*. As the best superficial character by which the rival claimants may be separated is that of size, let us consider this first.

Olivier (1789, p. 78) gave the following

measurements for *amalihea*: "Its body is scarcely three lines in length and a line and a half in width." Although Fabricius (1793, p. 325) did not give measurements, he referred to *amalihea* as half the size of *Apis amethystina*, later designated *Xylocopa amethystina*, which according to Lepeletier (1841, "Histoire naturelle des insectes, hyménoptères," vol. 2, pp. 182-183) is six lines in length. Thus the comparison of size that Fabricius gave seems to confirm the measurement cited by Olivier. Latreille (1804b, pp. 174-175) indicated the length as 5 mm. but subsequently ("1811"b, p. 294) expanded it to 6 mm. All of these measurements except that of Latreille (5 mm.) comes very close to what may be considered the maximum size of *fuscipennis* or the minimum size of *trinidensis*, represented by specimens with the segments compressed instead of expanded. I am inclined, however to agree with Vachal (1908, pp. 221-222) and Schrottky (1914, pp. 217-219) that the size indicated probably can better be reconciled with *fuscipennis* than with *trinidensis*, for while the variation in length of *fuscipennis* is moderate (ordinarily 4.75 to 6 mm.),¹ the range of size in *trinidensis* (6 mm. to 11 mm.)² has its average considerably above the three lines or 6 mm. mentioned in the descriptions.

One of the things that makes for hesitation, however, in definitely selecting *fuscipennis* as the claimant that best qualifies on the score of size is the painting of *amalihea* that Coquebert (1804, pl. 22, fig. 4) supplied to illustrate the description of Fabricius. Coquebert represented *amalihea* both life size and in enlargement. The portrait that is life size suggests a *trinidensis* of medium size. Moreover, and this I look upon as especially significant, the *amalihea* is depicted as being about as long as *Melipona favosa*, which appears as figure 3 on the same plate. In nature *Melipona favosa* and *Trigona trinidensis* are of very nearly the same length, whereas

fuscipennis is always smaller than *favosa*. Fabricius (1793, p. 325; 1804, p. 371) gave the source of the material on which his description of *amalihea* was based as "Mus. Dom. Olivier." Coquebert's figures were allegedly based also on this same material, for, as did Fabricius, Coquebert (1804, p. 97) gave the source of the material for *amalihea* as Mus. Dom. Olivier.

To offset, however, this strong evidence from Coquebert that true *amalihea* is the insect later designated *trinidensis*, we have the perhaps equally credible evidence in a drawing that Meunier (1804, pl. 13, fig. 13) prepared as accompaniment for Latreille's description. In this case, too, *amalihea* is supposed to be figured natural size, although the artist has failed so to render it. Indeed, the drawing, measuring 8.5 mm., accords neither with Latreille's specification of 5 mm. nor with nature. The actual size in this instance is, however, not the important thing; it is the relative size that counts, and the relatively smaller length of *amalihea* as drawn when compared to the large *Melipona favosa*, which occurs on the same plate (1804, pl. 13, fig. 12), leaves no doubt that it was *fuscipennis* rather than *trinidensis* that Meunier had before him. The relatively short wings of the *amalihea* of Meunier's drawing further confirm this interpretation, the wings of *trinidensis* being notably longer than those of *favosa*.

It seems likely that these early writers, or at least their artists, had access perhaps to both of the species in dispute. I have sometimes wondered indeed whether even among the material described by Olivier both species were not present. Such an assumption would go far to explain the divergent elements in his description. His material was obtained in part from French Guiana and in part from Surinam and may well, therefore, not have been uniform.³ Certainly while the length Olivier assigned his specimens favors the contention that they were *fuscipennis*, the description of the mandibles as brown basally, black apically is much more true of *trini-*

¹ Vachal (1908, pp. 221-222) indicated as the range of length of *amalihea*, interpreted as the same as *fuscipennis*, 5 to 7.5 mm. The maximum size he gave greatly exceeds that of the largest specimens (6.75 mm.) in the collections before me. Other writers (Ducke, for instance) give 6 mm. as the maximum.

² This is the range given by Friese for the *amalihea* of his conception, which is the equivalent of *trinidensis*.

³ Ducke (1925, p. 422) is of the opinion that *trinidensis* is not represented in the Guianas. In this connection the reader is referred to the section of the present discussion dealing with interpretations based on the geographic distribution.

dadensis; specimens of *fuscipennis* are almost invariably black basally and briefly striped with red just before the apex. On the other hand, the description of Olivier contains one significant structural character which applies admirably to *fuscipennis* but not quite so well to *trinidadiansis*. Olivier referred to the fore part of the head as flat ("plate"). Now, it is chiefly through its notably flat clypeus that *fuscipennis* is differentiated from most of its near relatives, including *trinidadiansis*, and Olivier's phrase seems, therefore, almost diagnostic. If one hesitates to accord it finality, it is out of deference to the fact that *trinidadiansis*, too, is at least relatively flat and that Olivier was not comparing *amalihea* with other *Trigona* but possibly with bees of rather prognathous appearance.

2. Interpretations based on biology. To support the interpretation that Olivier's *amalihea* is the same insect that Friese described as *fuscipennis*, Schrottky (1914, pp. 218-219) pointed out what he believed to be fundamental differences between *fuscipennis* and *trinidadiansis* in the selection of a nest site—the former building nests in the open, the latter constructing them in tree hollows. Olivier (1789, p. 79) clearly indicated that the nests of *amalihea* were built in the open, and this is the type of nest, too, that Bertoni (1911, p. 142) recorded for *amalihea* in the sense of *fuscipennis*. However, *amalihea* in the sense of *fuscipennis* is a more versatile architect than Schrottky believed it to be. In addition to the exposed nests that have been recorded, there are a number of examples of nests established in tree hollows (Burmeister,¹ 1853, p. 219; Ducke, 1925, p. 418; Salt, 1929, p. 440); in decayed beams (Burmeister, 1853, p. 219); or in old walls (Goudot, 1846, p. 713; Gronen, 1881b, p. 332).² Nests of *amalihea* in the sense of

fuscipennis are furthermore not infrequently built in termite structures.

With such evidences of adaptability on the part of *amalihea* in the sense of *fuscipennis*, one might suspect that *trinidadiansis* is not so inflexible in its selection of a nest site as Schrottky supposed. Several of the earlier records on which Schrottky relied indicate, indeed, that the nest is established in a tree hollow. Thus, the observations of Silvestri (1902b, p. 144), of H. von Ihering (1903, p. 204), and of Miranda-Ribeiro (cited by Ducke, 1925, p. 421) are all in accord that the nest of the bee here referred to under the name *trinidadiansis* is erected in hollow trees. On the other hand, an earlier record than any of these, that of Provancher himself (1888, pp. 344-345) in connection with the description of this species, disposes at the very start of any doubt that *trinidadiansis* is adaptable in the selection of a nest site. Thus Provancher recorded finding nests in empty pigeon holes in the church at Arima, Trinidad Island, and added that even when such nests were destroyed, the bees would build another nest in the same enclosure. Provancher then went on to say that later there was seen a like nest, very voluminous, on one of the buttresses of the cathedral at Port-of-Spain, and finally several nests were noted "attached to trees in the forest."

Myers (1935b, pp. 131-134), as did Provancher, made his observations in Trinidad, where he came upon a nest which he attributed to *silvestriana*, the name so often applied to *trinidadiansis* but in the present paper restricted to the Central American race of *trinidadiansis*. The nest was situated 18 feet above the ground in a large hog plum (*Spondias mombin*). After the tree had been felled and one of the limbs chopped away, "we found," according to Myers, "that the nest was entirely external, lodged in the first fork, between two huge branches, which formed two sides of the structure."

Very similar to this nest in its location is a nest of *trinidadiansis* figured by Weyrauch (1942, p. 63). This nest was lodged in the fork of a tree and clearly exemplified the exposed as contrasted with the concealed type

¹ Burmeister's *amalihea* may not be *amalihea* in the sense of *fuscipennis*, but it is far more apt to be that species than *trinidadiansis*, for Burmeister asserts it is "no larger than our house fly," which accords with *fuscipennis* but not with *trinidadiansis*.

² It is possible that the "*amalihea*" of Goudot and of Gronen, reported from New Granada (=Colombia), may be some bee other than *amalihea* in the sense of *fuscipennis*, for not only is the building site in old walls a somewhat unusual one for that species but Gronen indicated in a paper published subsequently (1881c, pp. 110-113) that the Colombian "*amalihea*" does not build

in trees, which is sharply at variance with the observations of Salt while in that country.

of nest construction. It was observed at Satipo, Peru. On the other hand, two nests of *trinidadensis* noted by the same observer in San Ramon; Valle de Chanchamayo, Peru, were not arboreal. One of them was in a hollow of a wall, with parts of the nest externally placed (pl. 5, fig. 1); the other was on the face of a cliff. Thus *trinidadensis* evidently is not so rigidly committed to an enclosed nest site as has been contended. The closely related *silvestriana* of Central America builds its nest by preference in the open.

As Schrottky (1914, pp. 217-219) has pointed out, Lepeletier (1836, pp. 426-427) described as *amalihea* what is probably *trinidadensis* although, curiously enough, Lepeletier specified that the mandibles are black at the base and testaceous at the apex, which, while the normal condition for *fuscipennis*, is the direct reverse in most specimens of *trinidadensis*. Lepeletier's description of the nest which he associated with this insect is, on the other hand, merely a fairly close transcript of the remarks published by Olivier; accordingly Lepeletier's statement is negligible when applied to the biology of *trinidadensis*.

The conclusion to which one is forced after a review of the above citations is that both *fuscipennis* and *trinidadensis* are adaptable builders and that the selection of the nest site does not furnish a reliable clue as to which insect is the proper claimant to be considered *amalihea*.

3. Interpretations based on the geographic distribution. Ducke (1925, p. 422) stated that *trinidadensis* was not represented in any of the Guianas. Were this *in toto* the case, it would constitute the most conclusive argument yet presented for rejecting the claims made on behalf of *trinidadensis* to rank as *amalihea*. Olivier's type material came from French Guiana and Surinam and, if *trinidadensis* does not exist in these states, obviously *trinidadensis* cannot be *amalihea*. Although the specimens of *trinidadensis* before me have been lent by a number of institutions, and some of these institutions have had expeditions in British Guiana and in Surinam, the only representatives from the Guianas among this material are a few specimens collected on the Kuyuwini River. Moreover, I have failed to find trustworthy

published records of the presence of *trinidadensis* in the Guianas. This negative evidence would indicate that in all probability *trinidadensis* is at least a rarity in that area. It may be that the stingless bee described by Barrère (1741, pp. 190-101) as *Apis Sylvestris* was no other than *trinidadensis*. Barrère's description is brief: "It is a species of black bees, very small, being only four or five lines at the most." Eighteen years later Fermin (1769, pp. 300-301) alluded under the same name to a social bee which he described as half the size of the European honeybee, being at the most five or six lines in length, and black. This description, too, fits *trinidadensis* rather better than it does *amalihea* (*fuscipennis*). Barrère's observations were made in French Guiana, those of Fermin in Surinam.

On the whole, weighing all of the evidence, it seems that *fuscipennis* has possibly a little better claim to be considered *amalihea* than has *trinidadensis*, and that interpretation is therefore here adopted.

The difficulties of interpreting the rival claims of the two contestants for the title of *amalihea* having been noted and decision made in favor of the smaller bee, it is in order to point out that occasionally specimens structurally identical with *amalihea*, as here interpreted, nevertheless show certain departures from the common run of specimens belonging to the species. For instance, two specimens of *amalihea* collected in the Botanical Garden, Paramaribo, Surinam, differ from the specimens of *amalihea* from other localities in lacking the red stripe on the mandibles.

There is also diversity of size among specimens. The smallest are those from El Encanto and La Chorerra, both in the Putumayo District of Peru. Their wing length is only about 5.25 mm., including the tegula, their thoracic width about 1.5 mm., and their body length about 3.75 mm. Because of the proportional reduction of the several parts, the malar space of the worker is in these specimens even more vestigial than is usually the case, and the apico-lateral extremities of the clypeus almost graze the eye.

At the other extreme are specimens from Lagunita de Aroa and San Julián, Venezuela, and from Río Frio, Colombia, that are notably large, with a forewing length, including

the tegula, of approximately 6.75 mm., and a thoracic width of as much as 2.25 mm. In these specimens the number of hamuli per lower wing tends to be at least six and is sometimes seven.

Although the specimens of maximum length present a contrast to those of minimum length, the intermediate specimens tend to link both extremes into a graded series as in *trinidensis*.

Variation may occur also in the shape of the seventh sternite of the male, as evidenced in figure 12.

Some of the specimens of *amalihea* from Kartabo, British Guiana, reported upon in this paper were collected by J. F. W. Pearson from the nest of a termite identified by Alfred E. Emerson as *Nasutitermes* (*N.*) *ephratae* (Holmgren). Previously Silvestri (1902a, p. 25; 1902b, p. 139; 1903, p. 212) had recorded *amalihea* under the designation *fuscipennis* from nests of *Eutermes rippertii* at Coxipò, in the State of Matto Grosso, Brazil. According to a communication from Emerson the species *rippertii* is confined to the West Indies, and the termite host should be designated *Nasutitermes* (*N.*) *breviocularis* (Holmgren). Professor Emerson has kindly supplied me with further information regarding the nest collected at Kartabo: "Two holes in nest used by bees. One at side below the middle had a flaring funnel-like entrance built by the bees, measuring about five inches at the outer diameter of the funnel. The other hole was at the end of a rounded projection below the funnel entrance. The outside of this was constructed by the termites, but the hole must have been kept open by the bees. I am not sure whether this hole was used as an exit or not. Ants of the species *Anochetus* (*Stenomyrmex*) *emarginatus* Fabricius (det. W. M. Wheeler) were also found in abundance occupying deserted cells of this termite nest."

Ducke has suggested (1925, p. 419) that the selection by *amalihea* of nest sites of varied character might be governed by local conditions. It is interesting in this connection that F. Nevermann in a letter written me from Costa Rica some time before his death stated: "I have not found any *amalihea* in open [that is, unsheltered] nests, always in the nests of termites." In contrast, all of the

nests of this species seen by Salt (1929, p. 440) in Colombia were "situated in hollow trees at a considerable height." Olivier, too, reported nests of only one type (unenclosed arboreal nests) from Surinam, and these were placed inaccessibly high, as were those noted by Salt. Thus there may be regional differences in the building habits of this species. The choice of high nest sites, so often apparently favored by *amalihea* and also often by *corvina*, is in contrast with the selection usually made by *fulviventris*, which is partial to nests in a tree low down towards the root system. However, Wheeler (1913, pp. 1-2) observed a nest of *amalihea* near Escuintla, Guatemala, that was in the base of a tree "only a few feet from the ground."

The most informing account of a nest of *amalihea* is that supplied by Salt (1929, pp. 438-441) regarding one located between 6 and 7.5 meters above the ground in the trunk of an aguacate tree (*Persea gratissima*) at Río Frio, Colombia. The nest was a large one, occupying a space about 110 cm. in length with a diameter varying from 18 to 22 cm., being thus notably larger than the exposed nests Olivier referred to in connection with his original description of *amalihea*. The nest included about 35 tiers of cells, but these tiers, while arranged horizontally, were not independent of one another. Instead, they "were connected to form a broad spiral, like a circular stairway. The entire comb, so far as it was followed, through twenty tiers, was complete in one unbroken helix." Salt estimated that there were at least 20,000 cells in the nest and the adult bees were "exceedingly numerous and bold." Twenty-six royal cells were counted. These were at the edge of the tiers of brood cells and, although usually attached to the comb, were in a very few instances fastened to the thin involucre that enveloped the brood portion of the nest or to the supporting pillars. The royal cells were only a little smaller than the pollen pots and the honey pots. The pollen pots, to the number of several hundreds, were massed in the lower part of the nest below the brood chamber, with only a very few honey pots intermixed. Above the brood, however, occupying a space some 15 cm. in upward extent, the honey pots were numerous and the pollen pots distinctly in the minority. In

addition to the two main groups of pots, there were at the extreme sides of some of the tiers small groups of honey and pollen pots that were fastened to the comb or to the involucre. Salt gives the dimensions of the individual pollen pots as only 1.5 to 1.7 cm. by 1 to 1.2 cm. In the nests reported by Olivier (1789, p. 79) on the basis of Renaud's observations the honey pots, at least, were about an inch long and six or seven lines in width, and their size seemed "very large when compared to the small stature of the insect."

Salt's account has an additional point of interest in that he lists no fewer than seven melittophiles from the nest. These included two species of phorid flies, *Pseudohypocera nigrofascipes* and *Melittophora salti*, and five species of mites: *Celaenosthanus trigonophilus*, *Trigonholaspis salti*, *T. columbiana*, *T. trigonorum*, and *T. amaliheae*, the last four all belonging to a new genus described by Vitzthum, who is also the author of the several species of *Trigonholaspis* listed.

The external architecture of *amalihea* nests is possibly no more standardized than is the selection of a nest site. What Burmeister interpreted as *amalihea* (1853, pp. 219-220) may possibly not have been *amalihea*. He described the nest entrance as almost resembling a cornucopia or, even more, the tip of a gigantic teapot. According to Marianno (1911, p. 79), the external projection of the entrance tube is almost cylindrical, but according to Wheeler (1913, p. 1), "a rather convoluted, spout-shaped entrance of black wax (cerumen)" jutting out between two buttresses gave access to a nest of this species in Escuintla, Guatemala. In contrast to the nests with projecting entrances was that minutely described by Salt (1929, pp. 438-441), which had "an oval opening about 4 cm. long and 2 cm. wide, without either external or internal entrance funnel."

Flowers visited by *amalihea* are of many kinds. Duce (1902b, p. 314) saw this bee "at all sorts of blooms, and often in large numbers even on Cyperaceae and Gramineae, collecting pollen." Previously he had noted (1902a, p. 325) a species of *Scleria* and one of *Parianea* (p. 326) as attracting it and mentioned (1902a, p. 325) its presence on *Dioclea lasiocarpa*, one of the Papilionaceae. Floral

visits to *Calopogonum caeruleum* and *Pontederia cordata* were recorded by Cockerell (1912c, p. 314), and the same author mentions (1916, p. 3) that *amalihea* was "abundant on the tall, sweet lilies" at Dunoon, British Guiana, according to the field observations of F. M. Gaige. Field notes of James Zetek indicate that *amalihea* has been collected on the castor oil plant, on *Asclepias*, and on the berries of *Coccoloba uvifera*. Salt (1929, p. 440) frequently observed *amalihea* on flowers of the banana, *Musa sapientum*, of *Antigonon leptopus*, and of several species of *Hibiscus*. At Río Frio, Colombia, he collected it from the blossoms of a species of *Bombax*. In Mexico A. Dampf noted *amalihea* on the flowers of *Marrubium*.

This bee ranks among those that are injurious to fruit, particularly bananas and *Citrus*. Thus Salt (1929, p. 440) stated: "This bee has earned an unenviable reputation in the banana plantations of Colombia on account of its habit of scarring the young fruit. Its mandibles are unfitted to make a breach in the flat surface of the banana skin, and its attack is, therefore, confined to the longitudinal ridges of young bananas before they have attained their plump maturity. From the triangular scars they form oozes slowly the sticky, milky sap of the green banana fruit, and this is apparently collected by the bees to mix with wax and resins in the formation of their structural cerumen." A field note attached to specimens of *amalihea* collected by A. Reyné in Paramaribo, Surinam, includes the expressive phrase "gnawing banana." Duce (1902a, p. 325) also reported *amalihea* under the name of *fuscipennis* as visiting *Musa*.

A field note by F. L. Gallego applying to specimens of *amalihea* collected at Puerto Valdivia, Colombia, is to the effect that this species is "injurious to *Citrus*." Among the stingless bees particularly ruthless in their attack on *Citrus*, M. Bates mentioned (1933, p. 47) *amalihea* and *silvestriana*, which he characterized as "perhaps the most striking pest of *Citrus* in the lowlands of Honduras." According to Bates these bees "are especially abundant on young trees, and seem to have a preference for grapefruit. They strip the bark from the main trunks of the trees and chew the terminal leaflets, apparently in an

effort to collect the sticky sap, probably to use in the construction of their nests." Ballou (1945, p. 129) listed *amalihea* as one of the harmful meliponid bees of Venezuela, indicating that it visits *Citrus sinensis* (Linnaeus) and *Punica granatum* Linnaeus.

The observation of Salt (1929, p. 440) that *amalihea* is attracted by honeydew of membracid nymphs is of interest. It confirms what Cockerell (1920c, p. 465) had previously called attention to: "In the U. S. National Museum is a piece of bark of the 'Mulungú tree,' obtained by Branner and Koebele in 1883 at 'Bnito, Prov. Pernambuco,' Brazil. On it are some homopterous insects (*Aethalion reticulatum* Fb., variety, det. Heide-mann), exactly the color of the bark. These are attended by *Trigona amalihea* and two species of beetles (det. Barber) of the genus *Conotelus* and *Cryptorhobalum*." H. Fleming also observed *amalihea* exploiting membracids in Venezuela. The association of stingless bees with membracids, first noted in the case of *Trigona (Oxytrigona) tataira* by H. Müller (1873, p. 201), has been reported only in isolated cases since then. However, the fact that the habit is shared by three such diverse groups of stingless bees as representatives of the subgenera *Trigona*, *Oxytrigona*, and *Paratamona* may indicate that it is more general than the limited number of instances recorded would seem to indicate (see Introduction, pp. 104-106).

According to Burmeister (1853, p. 219), *amalihea*, or what he interpreted as *amalihea*, is partial to sugar.

Rau (1933, p. 27) recorded *amalihea* as being attracted by the excrement of puma.

The honey of *amalihea*, it is claimed, is very sweet, very agreeable, and very fluid; its color is obscure reddish. It is so watery that it ferments a little time after having been removed from the honey pots, and it furnishes then a spirituous liquor which the Indians, according to the report of Renaud, enjoy (Olivier, 1789, p. 79; Lepeletier, 1836, p. 426; Girard, 1879, p. 724).

That *amalihea* is of an aggressive disposition is indicated by Burmeister (1853, p. 220), Silvestri (1903, p. 212), and Marianno (1911, p. 79). Salt, too, experienced its savage attacks: "Long before the nest opening was approached, and while I was still clambering

on the first limb, the bees attacked in numbers. They flew about me in hundreds with a buzzing audible many metres away, settled on my clothes, and entered every opening so that I soon had numerous bees inside my clothing biting me. They seemed deliberately to crawl to the base of the hair and bite sharply on the skin. Their bite is a distinct little pinch, and, while the effect is not lasting, to have fifty or more of these little black imps settled on various parts of one's body, all biting at the same time, is somewhat annoying and rather painful" (1929, p. 440).

Wheeler (1913, pp. 1-2) came upon a colony of *amalihea* that was "apparently about to swarm, as the air about the nest was full of bees flying back and forth in zig-zag paths like those described by some dancing empidid flies. A compact mass of the insects had settled to one side of the entrance of the spout."

The honeybee (*Apis mellifera* Linnaeus) is less aggressive at swarming time than in the ordinary course of things, and the bee-keeper at such a time can manipulate his bees with an incaution that would invite attack at any other time. One is interested to know how *amalihea* responds under similar conditions. "On putting my tweezers into this mass," wrote Wheeler, "I was at once enveloped in a cloud of loudly humming bees, which, however, did not settle on my body but kept darting against my face and hands, often falling over on their backs onto the ground or onto my clothing. They moved very rapidly and as if intoxicated. At the same time they emitted a distinct rancid-butter odor, like that of the ants of the genera *Tapinoma* and *Azteca*. On my moving away to a distance of about 40 feet, they all left me quite suddenly and returned to their nest."

Throughout the Santa Marta region of Colombia this bee is known as the "mapaitero" (Salt, 1929, p. 440), while Silvestri indicated that in Coxipò, Brazil, it bears the name of "abelha brava," shared also by *Trigona (Trigona) hyalinata* Lepeletier.

DISTRIBUTION

This species is of very wide distribution, extending from Mexico through all the Central American states and Panama deep into South America. It occurs in all the northern-

most countries of South America and is reported from most of the states of Brazil.¹ According to Bertoni (1911, p. 142; 1918, p. 224) it occurs in Paraguay, a country from which I have likewise seen specimens, and it is found also in Peru and Bolivia. Cockerell (1914b, p. 309) has reported it from Guayaquil, Ecuador, and I, too, have seen specimens from that locality.

In the collections before me specimens from the following localities are represented:

MEXICO: State of Vera Cruz: Santa Lucrecia and Atoyac (Schumann); Jesus Carranza, June, 1944 (M. Guerra). State of Tabasco: Teapa, March (H. H. Smith); Tiradero, 50 meters, Jan. 7, 1939 (A. Dampf). State of Campeche: Between Pajarral and La Lucha, 50 meters, "on the fresh leaves of some shoots from the base of a fallen tree," Jan. 10, 1939 (A. Dampf); Candelaria, Nov., 1944 (M. Guerra). State of Yucatan: Valladolid (Gaumer); northern Yucatan (Gaumer). State of Chiapas: Escuintla, 60 meters, on *Marubium* flowers, Nov. 11, 1930 (A. Dampf); between Escuintla and Finca El Zapote, 315-400 meters, "flying around the horse," Nov. 12, 1930 (A. Dampf); Tuxtla Chico, 295 meters, June 4, 1936, male. State of Oaxaca: Arroyo Choapam near Chiltepec, about 100 meters, Dec. 10, 1937; Tuxtepec, April 29, 1945 (T. C. Schneirla).

BRITISH HONDURAS: Belize, March 1, 1922 (H. F. Loomis).

GUATEMALA: Guatemala City (Champion); Gualan, Jan. 12, 1905 (C. C. Deam), Feb. 22, 1912 (W. P. Cockerell); Escuintla, Dec. 28, 1911 (W. M. Wheeler); Polochic River (Schwarz and Barber); San José (F. Knab); Chiquimulilla, Dept. of Santa Rosa, 300 meters (R. Liche); Cacao, Trece Aguas, Dept. of Alta Vera Paz (Schwarz and Barber); Chicacao, Feb. 8, 1930 (D. M. Bates); El Salto, Escuintla, June 28, 1934 (F. X. Williams).

HONDURAS: Tegucigalpa, April 30, 1917 (F. J. Dyer); La Ceiba, Oct. 8, 1916, Dec. 19, 1916 (F. J. Dyer); Carmelina (W. M. Mann); Tela, Lancetilla Creek, March 16, 1923 (T. H. Hubbell); Tela, Guimas Dist., May 1, 1923 (T. H. Hubbell); Tela, Dakota Farm, May 19, 1923 (T. H. Hubbell); Corocito, April 3, 1924 (J. Bequaert); Prieta, April 5, 1924 (J. Bequaert); Sangrelaya, April 13, 1924 (J. Bequaert); Cantaranas, Río Choluteca, 2200 feet, Aug. 3, 1920

(Honduras Exped. of the Academy of Natural Sciences of Philadelphia).

EL SALVADOR: Sonsonate, Aug. 19-20, 1905 (F. Knab).

NICARAGUA: Chinandega (Baker); Chontales (Janson); Cosiguina Slope, July 8, 1932 (M. Willows, Jr.); north side of Cosiguina Volcano, Dec. 23, 1938 ("Zaca" Exped.).

COSTA RICA: Port Limon, March, 1915; Guapiles, July, 1915 (D. E. Harrower); Hamburg Farm, April 4, 1937, including males, in *Nasutitermes* nest, and May 23, 1937 (F. Nevermann); Matina, July, 1937, No. 187 (A. Alfaro); Port Parker, Elena Bay, Jan. 13, 1938 ("Zaca" Exped.).

PANAMA: Bugaba, 800-1500 feet (Champion); David (Champion); Alhajuela, April 11, 1911 (A. Busck); Cabima, May 18, 1911 (A. Busck); La Chorrera, April 12, 1912 (A. Busck); Chitré, April 25, 1921, on castor oil plant (J. Zetek); Parita, April 27, 1922, on berries of *Coccoloba uvifera* (J. Zetek); Panama City, July 26, 1921, on *Asclepias* (J. Zetek), Jan. 24, 1945, and Feb. 1, 1945 (C. D. Michener); Las Sabanas, March 2, 1923 (W. M. Wheeler), Nov. 17, 1923 (F. E. Lutz), July 7, 1924 (N. Banks); Progreso, Chiriqui Province, April 14-15, 1923 (F. M. Gage); Bella Vista, July 2, 1924, July 6, 1924, Aug. 7, 1924, Aug. 9, 1924 (N. Banks); 8 miles east of Porto Bello, Feb. 9, 1930 (T. O. Zachokke); Pecora, March 19, 1933 (H. F. Schwarz); Old Panama, Feb. 4, 1945 (C. D. Michener).

CANAL ZONE: Tabernilla, July 24, 1907 (A. Busck); Empire, May 8, 1909 (A. H. Jennings); Paraiso, Jan. 17, 1911, March 25, 1911 (A. Busck); Corozal, March 1, 1912 (A. Busck), Feb. 23, 1914 (T. Hallinan), Jan. 22, 1929 (C. H. Curran), Nov. 17, 1930 (H. F. Schwarz); Ancon, Feb. 26, 1914 (T. Hallinan), April 14, 1924 (J. Zetek), July 18, 1924, Aug. 9, 1924 (N. Banks); Punta Patilla, Feb. 22, 1923 (W. M. Wheeler), Jan. 15, 1929 (C. H. Curran), June 20, 1930 (H. F. Schwarz); Red Tank, March 1, 1932, males (W. M. Wheeler), June 30, 1924 (N. Banks); Barro Colorado, Nov. 13, 1923 (F. E. Lutz), July 16, 1924, July 18, 1924, July 20, 1924, July 24, 1924 (N. Banks), Dec. 21, 1928 (C. H. Curran), Nov. 22, 1930 (E. I. Huntington), Feb. 9, 1936 (W. J. Gertsch); Chiva Chiva Trail, Nov. 18, 1923 (F. E. Lutz), Nov. 24, 1930 (H. F. Schwarz), March 11, 1933 (H. F. Schwarz); Ft. Sherman, July 3, 1924 (N. Banks); Mt. Hope, July 8, 1924 (N. Banks); Gamboa, July 9, 1924 (N. Banks); Frijoles, July 10, 1924 (N. Banks).

COLOMBIA: Aracataca, Magdalena, "in heavy forest with dense undergrowth," Aug. 10, 1920; El Banco, Magdalena Valley (C. Allen); Río Frio, Magdalena, March 20 (P. J. Darlington, Jr.), at *Bombax* sp., Feb. 1, 1927 (G. Salt), scarring bananas, Nov. 21, 1926 (G. Salt), at *Musa sapientum*,

¹ Duce (1925, p. 419) reported its presence in the Brazilian States of Amazonas, Pará, Maranhão, Ceará, Matto Grosso, Goyaz, Río de Janeiro, São Paulo, and Santa Catharina. Cockerell (1912b, p. 60) saw specimens from Rio Grande do Norte and Parahyba do Norte.

Sept. 27, 1927 (G. Salt); Ciénaga, Magdalena, Feb. 6, 1927, at "honeydew" of membracid nymphs (G. Salt); Santa Anna, Feb., 1924 (W. M. Mann); Carthagena; Buenaventura, Feb. 22, 1935 (H. F. Schwarz); Puerto Valdivia, Jan., 1942, "injurious to citrus" (F. L. Gallego).

VENEZUELA: San Julián, July 19, 1900 (M. W. Lyon, Jr.); Lagunita de Aroa, at 2000 feet, Dec. 1910 (M. A. Carriker); Río Amakura, Feb., 1931 (J. G. Myers); Maracay, Dec. 10, 1930; Calabozo, Dec. 27, 1930; San Juan, May 31, 1934 (Farenholtz); Barinitas (P. J. Anduze); Caripito, March 13, 1942 (H. S. Fleming).

TRINIDAD: May, 1924 (L. E. Cheesman).

BRITISH GUIANA: Rockstone, July 9, 1911 (F. E. Lutz), June 1, 1929 (J. Ogilvie); Portaro Landing, Aug. 18, 1911 (F. E. Lutz); Chenapowu to Saveritik, Aug. 21, 1911 (F. E. Lutz); Essequibo River, July, 1921 (A. Busck); Kartabo, Aug. 5, 1920 (W. M. Wheeler), June, 1922 (M. D. Haviland), Aug. 2, 1924 (J. F. W. Pearson); Camaria, July 31, 1924 (J. F. W. Pearson); Mabaruma, Northwest District, March, 1931 (J. G. Myers); Matope, July 23, 1924 (J. F. W. Pearson); Kalacoon, Bartica District, July 15, 1926 (J. F. W. Pearson); Kangaruma, May 23, 1929 (J. Ogilvie); Tumatumari, May 31, 1929 (J. Ogilvie); Marshall Fall, Mazaruni River (J. Ogilvie); Hosororo, Northwest District, February, 1931 (J. G. Myers); Kamaria Landing, Cuyuni River, Nov. 23, 1929 (Oxford Univ. Exped.); Wismar, Dec. 23, 1933 (A. S. Pinkus); Rossfield, Berbice River, Jan. 12, 1936 (J. Ogilvie); between Membaru Creek and Kurupung River (upper Mazaruni District), Feb. 22, 1939 (A. S. Pinkus).

SURINAM: Paramaribo, Jan. 21, 1920, males, April 3-18, 1927 (Cornell Univ. Exped.); Botanical Garden, Paramaribo, "gnawing banana" (A. Reyné); Sint Barbara Pln., April 11-16, 1927 (Cornell Univ. Exped.); Kwakoegeon, Saramacca River, June 14, 1927 (Cornell Univ. Exped.).

BRAZIL: State of Amazonas: Río Içá-Putumayo, Aug. 11, 1920 (Cornell Univ. Exped.). State of Pará: Furo de Ressaco, Río Amazonas, night of Sept. 10, 1920 (Cornell Univ. Exped.); Santarem (H. H. Smith); Belem, July, 1904 (A. Ducke), and July 13, 1924 (J. Bequaert); near Belem (H. B. Merrill); Prata, June 30, 1919 (H. Parish). State of Bahia: Tapará, June 24, 1915. State of Matto Grosso: Chapada (probably Sant'Anna do Chapada, near Cuyabá, Jan. (H. H. Smith); Descalvados, Rio Paraguay, altitude 560 feet, July 8, 1931 (J. A. G. Rehn). State of Minas Gerais: Barro Alto, Nov., 1931 (José Blaser). State of Pernambuco: Pernambuco, Jan., 1883, Jan. 21, 1920, males; Sanharó. State of São Paulo: Jundiahy, 1897. State of Rio de Janeiro: Rio de Janeiro, Aug., 1915 (P. G. Russell), Nov. 11-15,

1926 (A. Seitz); Tijuca, Oct., 1919 (Cornell Univ. Exped.). State of Santa Catharina: Massaranduba-Blumenau, Sept.-Oct., 1935, including queen (K. Schmith).

PARAGUAY: Puerto Bertoni.

PERU: Hda. San Juan, Colony of the Perené, June 19, 1920; El Campamento, Colony of the Perené, June 19, 1920; mouth of Río Cotuhé, Aug. 12, 1920; El Encanto; (The Peruvian specimens were collected by the Cornell Univ. Exped.)

BOLIVIA: Blanca Flor, Río Beni, Jan. (W. M. Mann); Ivon, Río Beni (W. M. Mann); Cavinás, Feb. (W. M. Mann).

ECUADOR: Milagro, Sept. 29, 1922 (F. X. Williams); Guayaquil, Nov. 25, 1922 (F. X. Williams).

Trigona (Trigona) recursa F. Smith

? *Vamos embôra*, SPIX AND MARTIUS, 1828, p. 542.

Trigona recursa F. SMITH, 1863a, pp. 504, 508, pl. 20, fig. 15.

? "Feiticeira" or "Vamo-nos-embora," ANONYMOUS, 1878b, p. 74.

? *Melipona recursa*, PECKOLT, 1893, p. 580.

? *Melipona recursa*, PECKOLT, 1894, p. 223.

Melipona recurva, DALLA TORRE, 1896, p. 583.

? "Feiticeira," or "Vamo-nos-embora," H. VON IHERING, 1903, p. 272.

? *Trigona recurva*, H. VON IHERING, 1904b, pp. 384-385.

? *Trigona recurva*, GRÜNBERG, 1904, p. 17.

Trigona recursa, COCKERELL, 1912b, p. 60.

Trigona recursa, SCHWARZ, 1940, pp. 1, 4-5.

Trigona recursa, MOURE, 1944a, p. 73.

WORKER

DIAGNOSTIC CHARACTERS: Black. Mandible five toothed, usually black with a narrow red band just behind the apex. Length of malar space comparable with width of flagellum. Clypeus only a little less flat than that of *amalthaea* and a little more than one-third as long as its greatest width. Clypeus, supraclypeus, and scape with black bristle-like hairs. Hind tibiae with a feeble inwardly placed angle at the apex posteriorly. Wings subhyaline.

HEAD: Black or mainly black. The facial quadrangle wide, the distance between the compound eyes at a level just below the middle ocellus about equal to the distance between the anterior ocellus and the apex of the clypeus. The compound eyes fairly strongly convergent below, the distance that separates them at their level of greatest approximation

(below) being about six-sevenths that of their divergence at the level just below the anterior ocellus. The clypeus raised only very slightly above the level of the sides of the face, very nearly flat to subarcuate over most of its surface, very slightly foveate medianly at the apex. The width of the clypeus almost

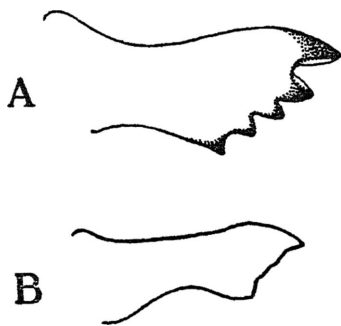


FIG. 13. Mandible of worker (A) and male (B) of *Trigona* (*Trigona*) *recursa* F. Smith. Both mandibles are inverted in the figure.

three times as great as its length; its anterolateral extremities separated from the compound eye by approximately the width of the flagellum. The labrum simple. The mandibles (fig. 13A) armed with five teeth (not three- or four-toothed as erroneously stated in original description). The length of the malar space at its middle comparable with the width of the flagellum. The distance from each lateral ocellus to the nearest eye a trifle greater than that which separates one lateral ocellus from the other. Carina behind ocelli usually rather strongly developed and somewhat thin edged (compared, for instance, with *amalihea*) rather than blunt. The clypeus, front, vertex, and lower one-third of genal area more or less moderately shiny. The clypeus covered relatively lightly with silvery gray appressed microscopic hairs; the sides of the face with similar, somewhat denser hairs, and to a lesser extent such hairs are also on the front; the genal area silvery gray pruinose on its upper two-thirds. The longer, erect, and coarser hairs of the head black, being distributed over the clypeus and supraclypeus in addition to the front, vertex, lower one-third of genal area and inferior margin of mandibles; exceptionally there may even be a few short

dark bristles among the dense silvery gray hairs of the sides of the face and the upper two-thirds of the genal area. The scape with somewhat coarse, erect, black, bristle-like hairs, similar to those on the clypeus but as a rule not so long, being in most cases (with the exception usually of those towards the base of the inner face of the scape) somewhat shorter than the scape is wide. The mandibles usually mostly black with a subapical red stripe as in *amalihea*, in other cases (even in specimens that do not give other evidence of being callows) largely or wholly red except for the black teeth. The labrum similarly variable from black to reddish. The clypeus usually black like the rest of the head but sometimes with two more or less symmetrical red marks. The antennal sockets ferruginous to brownish. The flagellum brownish below, darker above; the scape usually black but sometimes streaked with brown in front.

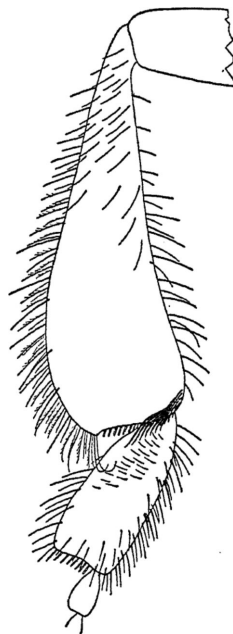


FIG. 14. Hind tibia and metatarsus of worker of *Trigona* (*Trigona*) *recursa* F. Smith. Drawing by Elena Feld.

THORAX: Black, of somewhat subdued sheen on the mesonotum and scutellum due to the rather dense brownish to dark grayish tomentum. The tomentum a little more grayish on the sides of the thorax and on the

sides of the propodeum. The erect simple hairs black, their distribution and relative length as indicated in the description of the subgenus *Trigona*.

LEGS: Black to now and then more or less brownish, and at least the apical joint of the tarsi almost invariably ferruginous and the intermediate tarsal joints frequently more or less ferruginous. The hind tibiae (fig. 14) relatively slender, clavate in outline, wider at the apex than at the base but a little narrower throughout than in *amalihea*; their anterior lateral contour gently emarginate, their posterior lateral contour rather more strongly convex; their apex with an inconspicuous angle anteriorly that bears the comb, this followed by a bulge in the apical contour, and beyond this bulge the apex is slightly emarginate with the result that there is a feeble inwardly placed angle where the apical contour runs into the posterior contour of the joint; the outer face of the hind tibiae so gently arched over the basal two-thirds as to approximate a flattened condition, but even more decidedly flattened to somewhat excavated on the apical one-third, the excavation appearing to be a shade deeper than in *amalihea*. The flattened area margining the under side of the hind tibiae posteriorly less than one-third the width of the joint near the apex. The hind metatarsi about two-thirds as wide as the hind tibiae, rather parallel sided, a little constricted at the base, their posterior apical extremity almost rectangular to slightly produced downward. The hairs of the legs predominantly black but with the following relatively minor exceptions: the hairs on the fore trochanters beneath usually pale; the rather long plumose hairs intermixed with the slightly longer erect black hairs on the outer face of the middle tibiae usually somewhat dark grayish to blackish; the microscopic but stubby hairs on the elevated part of the under side of the hind tibiae and adjacent apical part beneath of the associated femora silvery gray; the suboval sericeous patch at the base of the under side of the hind metatarsi silvery gray but its hairs often discolored owing to their being glazed over by sticky matter; the metatarsal brushes black to copper colored. The relative length of the hairs and their distribution as noted in the description of the worker of the subgenus *Trigona*.

WINGS: Subhyaline, more transparent than those of *amalihea*, with the median and marginal cells only a little darker, if at all, than the other cells. The venation and stigma brownish to now and then fuscous. The tegulae blackish. The vestiges of the transverse cubital veins usually moderately defined to more or less obscure. First discoidal cell about four-fifths as long as the marginal cell. Number of hamuli on each wing varies from four to six but in the great majority of cases is five. Of 173 wings examined, 154 had five hamuli, three had four hamuli, and 16 had six hamuli, an average of 5.08.¹ The tegulae black or blackish.

ABDOMEN: Black or blackish, as a rule not telescoped and elongate rather than compact, narrower than thorax, trigonate. The hairs black. Tergites 2 and 3 with a narrow band of microscopic tessellation along the apex, corresponding with the presence of appressed or semi-appressed hairs. Feeble tessellation also sometimes traceable along the apex of tergites 4 and 5 as well as scant appressed hairs. More conspicuous are the longer erect hairs over approximately the apical half of tergites 4 and 5 and such hairs are also on tergite 6. Approximately the apical half of the sternites with erect black hairs at the middle and a low growth of sericeous hairs, silvery gray in some lights, on each side of the middle of sternites 3 to 6. When the abdomen is telescoped, the hair bands form a continuously hairy surface.

MEASUREMENTS: Length 4.25 to 5.75 mm.; width of thorax about 1.75 mm.; length of forewing, including tegula, about 6 mm.

QUEEN

Unknown.

MALE

HEAD: Black. The facial quadrangle narrower than in the worker. The distance from one eye to the other at their level of closest

¹ Among the workers from San Ramon, Peru, there are relatively fewer specimens with six hamuli than is the case among the workers from some other localities, notably Igarapé-Assu, Brazil. As all the males examined were from San Ramon, it may be that the average of five hamuli reported for the male applies only to the male of that locality and is an understatement, but at best the averages given can only be approximate, owing to the inadequate number of specimens available for the count.

approximation (below) is only about five-sevenths the length of the eye, whereas in the worker the shortest distance between the eyes approximates the length of the eye. The clypeus and supraclypeus barely more prominent than those of the worker, the apicolateral extremities of the clypeus somewhat acute and almost attaining the rim of the eye, being separated from it by rather less than one-half of the width of the flagellum at the apex. The length of the clypeus about one-half its greatest width. The labrum simple. The mandibles (fig. 13B) acutely pointed at the outer extremity of their apical edge, which recedes inward and is edentate or only very obscurely dentate with an obtuse angulation at the inner extremity; a red stripe immediately behind the apical edge of the otherwise black mandibles and sometimes including the apical edge. The malar space very greatly reduced but not quite obsolete, the inner angle at the base of the mandible and the rim of the eye being kept distinct by a very thin line of separation. The distance between the lateral ocelli greater than that between each lateral ocellus and the nearest compound eye. The carina behind the ocelli usually rather strongly developed and relatively thin edged (less blunt, for instance, than the carina of *amalihea*). The head only about as hirsute as that of the worker of *recursa* and barely more so than that of the male of *amalihea*. In addition to the silvery gray appressed tomentum that covers rather densely the clypeus, sides of face, and front, there are black erect hairs on the clypeus, supraclypeus, scape, front, sides of face, vertex, lower part of genal area, labrum, and fringing the mandible below, but these dark hairs, with the exception of those on the vertex, are less conspicuous when the face is viewed from in front than is the silvery gray tomentum, which extends also to all but the lower extremity of the genal area. The black hairs of the scape longer than the mainly pale hairs on the scape of the male of *amalihea*, although pale hairs, even if dwarfed by the black hairs, are present also on the scape of the male of *recursa*. The antennal sockets ferruginous; the otherwise black scape with a ferruginous stripe in front (sometimes obscure); the flagellum black above and sometimes also below but in other cases with the

lower surface more or less ferruginous.

THORAX: Black, of somewhat subdued sheen, especially on the mesonotum, due to the presence of dark grayish to blackish tomentum. The erect hairs of the thorax black.

LEGS: Black, with the apical tarsal joint, and frequently the intermediate tarsal joints as well, more or less ferruginous. The hind tibiae along their anterior lateral contour feebly concave; their posterior lateral contour much more emphatically convex; the contour of their apex approximating the round; their exterior face rather arched but the posterior part of the apex of this exterior face a little more flattened than in the male of *amalihea*. The greatest width of the hind tibiae (near the apex) about four-fifths that of the conspecific worker at the corresponding level. The hind metatarsi approximately three-fourths of the width of the hind tibiae, the posterior apical angle slightly acute to rounded. The hairs of the legs predominantly black or blackish with the following relatively minor exceptions: usually the hairs on the under side of at least the fore trochanters are whitish; and the microscopic but stubby hairs on the elevated part of the under side of the hind tibiae and adjacent apical part beneath of the hind femora as well as the sericeous hairs of the rather small differentiated area at the base of the inner face of the hind metatarsi silvery gray; the plumose hairs (when present) on the outer face posteriorly of the middle tibiae sometimes dark grayish to brownish rather than black (as are also apt to be the plumose hairs of the posterior lateral fringe of the hind tibiae), but these hairs as a rule sparser and shorter than in the corresponding area of the worker and in some specimens even lacking; the metatarsal brushes black to, in some lights, copper colored. The mainly plumose fringe along the posterior lateral contour of the hind tibiae consists of hairs that are relatively short, distinctly less than half as long as the hind tibiae are wide at their widest. The distribution of the simple black hairs in general and their relative length approximately as indicated in the description of the male of subgenus *Trigona*.

WINGS: Subhyaline, more transparent than those of *amalihea*, with the median and marginal cells only a little darker, if at all, than the other cells. Tegulae blackish. Number of

hamuli per lower wing ranges from four to six but is almost invariably five. Of 185 wings examined, 181 had five hamuli, while only two wings had as few as four hamuli and only two wings as many as six, an average of five hamuli.

ABDOMEN: Black or blackish, somewhat tapering from base to apex, but even the base distinctly narrower than the thorax. Tergites for the most part strongly shiny but, as in the worker, there is a narrow apical band of

collection, identified by Smith himself as *re-cursa*, is at Oxford University, and a further specimen from the F. Smith collection similarly identified was recently donated to the American Museum of Natural History by T. D. A. Cockerell. *Trigona recurva* was described from Brazil.

DISCUSSION

In many respects this species is much like *amalihea*. Its clypeus is only a little less flat

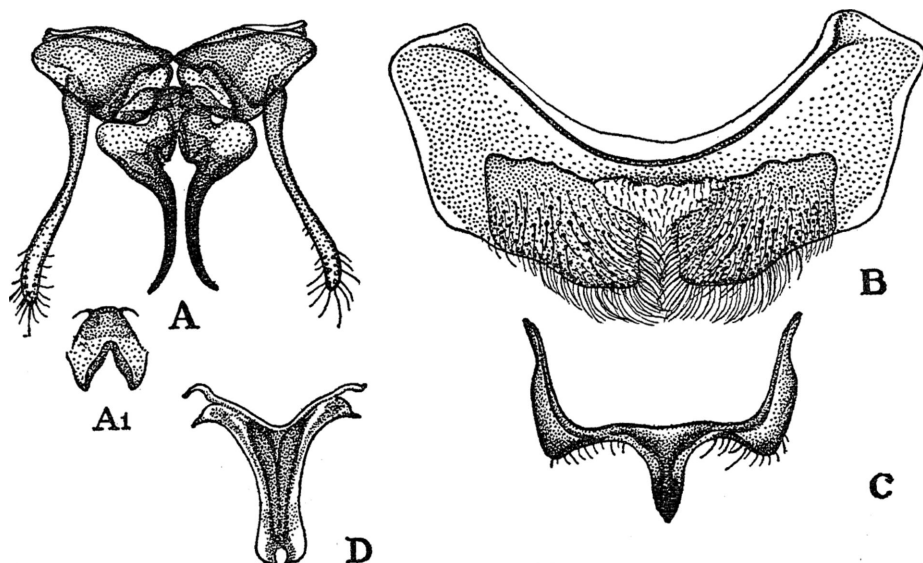


FIG. 15. Abdominal parts of the male of *Trigona* (*Trigona*) *recurva* F. Smith. A. Genitalia (chitinized parts only). A1. Dorsal plate that supports laterally the bases of the sagittae. B. Sternite 5. C. Sternite 6. D. Sternite 7. All based on specimens from San Ramon, Peru. Drawings by Shirley H. Risser.

feeble tessellation on tergites 2 to 4 covered by microscopic appressed dark hairs. Tergites 5 and 6 with similar but a little coarser, somewhat punctate sculpturing over the apical half of each of these tergites where the longer erect to semi-erect black hairs emerge (such hairs, somewhat shorter and less conspicuous, occur also as a rule on tergite 4). Tergite 7 with a fringe of black hairs apically. The sericeous hairs of the venter rather dull grayish. (Fig. 15).

MEASUREMENTS: Length 5 to 7 mm.; width of thorax about 1.75 mm.; length of forewing, including tegula, about 6 mm.

TYPE MATERIAL

The type is in the British Museum (Natural History). A specimen from the F. Smith

than that of *amalihea*, being barely foveate at the apex. Its scape, in contrast to the fine downy covering of the scape of *amalihea*, has short, black, bristle-like hairs. The clypeus also has stiff, erect, black hairs. The malar space seems to be a very little wider than in the older species. While the mandibles of *amalihea* are almost always black, striped with red just behind the apex, *recurva* shows considerable variability in this respect even among the specimens of a single locality, some individuals having mandibles corresponding with the coloration prevalent in *amalihea*, while others have largely reddish or brownish mandibles. Possibly these survivals of red are the last vestiges of the callow state. The insect is smaller and of more dainty structure than *amalihea*, and its hind tibiae

are more slender. Owing to the fact that the abdomen is rather more slender and elongate than the usually compact abdomen of *amalihea*, specimens of *recurva* may measure the same length as specimens of *amalihea* that have the abdomen especially contracted. However, the thorax width of *recurva* is always less than that of *amalihea*, and the two insects, when placed side by side, can be differentiated even by the unaided eye because of their difference of stature.

By its more dainty stature *recurva* is readily differentiated also from *corvina*, from which it differs furthermore in having a less arcuate clypeus and distinctly narrower hind tibiae. From both *amalihea* and *corvina* it can furthermore be separated by the more hyaline condition of its wings, the wings of the other two species having a distinctly deeper stain.

I have had opportunity to examine, in addition to the type specimen, the specimen identified at Oxford, and the one from the F. Smith collection in the American Museum. All of these specimens have quinquedentate mandibles. F. Smith's statement to the effect that the mandibles have "three or four stout acute teeth at their apex" is misleading.

Dr. W. Weyrauch has sent me the following description of a nest (pl. 5, fig. 3) of this species that he observed at San Ramon, February 25, 1940: "Nest in earth at the foot of an old tree. A protruding tunnel-like structure of black granular resin holds fast to the ground dead leaves that are lying about. The nest entrance is 5 cm. wide and 7 cm. long. The tunnel-like structure in its entire extent is 10 cm. wide and 14 cm. long. The tunnel enters into a hollow root, which is used as a passage-way to the nest."

The nest was one of three located about the base of an old tree (Oropel) in a shady coffee plantation. The other two nests were those of bees of the subgenus *Partamona*.

Very similar in location was apparently a second nest (No. 158) of *recurva*, likewise observed in San Ramon, regarding which Weyrauch's field notation reads: "Nest in earth under root of tree. Flight tube widely open, funnel-shaped." Yet another nest seen by Weyrauch in the same locality was likewise subterranean.

It may be that this subterranean habit is characteristic of a restricted geographic area

or at least is predominant in such an area, and that in other regions *recurva* selects nest sites of different character. At any rate, according to Peckolt (1894, p. 223), writing from southern Brazil, tree hollows are selected by *recurva* as nesting places in that area. It is, of course, possible that Peckolt, several of whose interpretations of species are open to question, may have picked the wrong bee to which to attach the name *recurva*. F. Smith, who described *recurva* (1863a, p. 504), gave as its popular name "vamos embôra" (let us be off). Peckolt, on the other hand, recorded its vernacular name as "feiticeira" or witch (1893, p. 580; 1894, p. 223). Possibly Smith and Peckolt are speaking of two different bees. Challenging such a conclusion is, however, H. von Ihering's association of both of these vernacular names with the same bee (he does not give its scientific name). This bee, he stated, occurs in São Paulo and its honey is potently inebriating (1903, p. 272; 1904b, pp. 384-385). Among the stingless bee specimens that I have examined from southern Brazil I have found no representatives of *recurva*.

DISTRIBUTION

While *amalihea* extends throughout Central America into Mexico, *recurva* seems not to be represented in this region. It would seem to be of rare occurrence in the northernmost states of South America. It is known, however, from British Guiana and has been taken far up in Brazil, in the State of Pará. It has been affirmed, too, that *recurva* occurs in southern Brazil. The center of population of *recurva* would seem to be on the west coast of South America in such countries as Peru and Bolivia.

The following localities are represented in the collections before me:

BRITISH GUIANA: Kuyuwini River, Nov. 22, 1937 (W. G. Hassler); Essequibo River, at source (J. Ogilvie).

BOLIVIA: Santa Elena, Aug. (W. M. Mann); Tumupasa, Dec. (W. M. Mann); Ixiamas, Dec. (W. M. Mann); C. Esperanza, Río Beni, March (W. M. Mann).

PERU: Yurimaguas, April 8, 1920 (H. Parish); La Merced, Río Chanchamayo, June 17, 1920 (Cornell Univ. Exped.); El Campamento, Colony of the Perené, June 22-26, 1920 (Cornell Univ. Exped.); La Chorrera to La Sombra, Putumayo

District, Aug. 21, 1920 (Cornell Univ. Exped.); San Ramon, at meat, Feb. 16, 1940 (W. Weyrauch); San Ramon, at a puddle, male, Feb. 17, 1940 (W. Weyrauch); San Ramon, from a nest, including many males, Feb. 25, 1940 (W. Weyrauch); Satipo, 600 meters, Aug. 10, 1940 (W. Weyrauch).

ECUADOR: Tena, Feb. 14 and Feb. 17, 1923 (F. X. Williams); Napo, Río Pana, April 8, 1923 (F. X. Williams).

BRAZIL: State of Pará: Igarapé Assú, July 15, 1919 (H. Parish); Belem, July 15, 1924 (J. Bequaert); Furo de Ressaco, Rio Amazonas, night of Sept. 10, 1920 (Cornell Univ. Exped.); Rio Japurá (Roman). State of Matto Grosso: Chapada (probably Sant' Anna do Chapada), (H. H. Smith). State of Minas Gerais: Barro Alto, Nov., 1931 (José Blaser). Also from Maruru (H. H. Smith), presumably in Brazil.

Trigona (Trigona) hypogea variety
hypogea Silvestri

? *Trigona argentata*, KRIECHBAUMER, 1900, p. 99.

Trigona hypogea SILVESTRI, 1902b, pp. 132-133, pl. 1, fig. 16.

? *Trigona argentata*, SCHULZ, 1904a, p. 262 (identified by H. Friese).

? *Trigona argentata*, SCHULZ, 1904b, p. 827 (identified by H. Friese).

Trigona recursa, COCKERELL, 1920c, pp. 460, 464-465, 467.

Trigona recursa a, LUTZ, 1924a, pp. 205, 208, 212, 215.

Trigona (Trigona) hypogea, SCHWARZ, 1938, pp. 442, 455.

WORKER

DIAGNOSTIC CHARACTERS: Black. Mandible five toothed, in mature specimens probably as a rule black with narrow red band behind apex. Length of malar space subequal to width of flagellum. The clypeus completely flat, its greatest width almost three times as great as its length. Coarse black hairs on clypeus and supraclypeus; black hairs also on scape. Hind tibiae narrow, gradually and only very moderately widened from base to apex, with their apical contour uniformly or nearly uniformly rounded posteriorly as well as anteriorly. Wings subhyaline.

HEAD: Black or predominantly black. The facial quadrangle wide, the distance between the compound eyes at a level just below the middle ocellus about equal to the distance from the middle ocellus to the apex of the

clypeus. The clypeus barely raised above the level of the sides of the face, absolutely flat and even over most of its surface. The compound eyes fairly strongly convergent below, the distance that separates them at their level of greatest approximation (below) being about as six is to seven when compared with their divergence at the level just below the middle ocellus. The width of the clypeus almost three times as great as its length; its anterolateral extremities separated from the compound eye by less than the width of the flagellum. The labrum simple. The mandibles

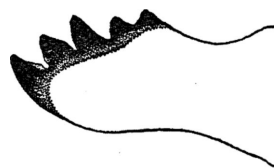


FIG. 16. Mandible of worker of *Trigona (Trigona) hypogea* Silvestri. Drawing by Elena Feld.

armed with five teeth (fig. 16). The malar space measured from the lower extremity of the eye to the base of the mandible at its middle subequal in length to the width of the flagellum. The distance between the lateral ocelli barely less than the distance that separates each lateral ocellus from the nearest compound eye. The carina behind the ocelli moderately developed to low and somewhat blunt. Clypeus, front, vertex, and lower one-third of genal area more or less shiny. The clypeus covered relatively lightly with silvery gray appressed microscopic hairs; the sides of the face with similar, somewhat denser hairs, and to a slightly lesser extent such hairs also cover the front; the genal area silvery gray pruinose on its upper two-thirds. The longer and coarser hairs of the head predominantly black. The hairs of the clypeus and supraclypeus relatively long and fairly numerous, in nearly all cases longer and coarser than the erect black hairs of the scape but shorter than those of the vertex, those on the lower one-third of genal area, and those fringing the mandibles below, the last mentioned being pale to copper colored. The hairs on the scape for the most part or all shorter than the scape is wide. The mandibles sometimes black, briefly streaked with vivid red behind the apex as in *amalihea* (true of all the

Bolivian specimens before me, even callows, and of the Peruvian specimens of the typical variety), but sometimes largely or wholly brownish or reddish except for the black teeth (true of certain of the British Guianan specimens, which may, however, have not attained their complete adult coloration). In callows the clypeus is sometimes brown even when the other parts of the face are black, and frequently there occur even on the black

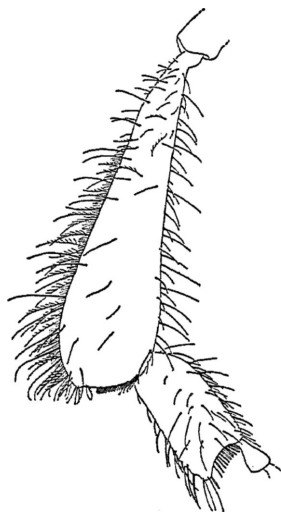


FIG. 17. Hind tibia and metatarsus of the worker of *Trigona* (*Trigona*) *hypogea* Silvestri. Drawing by Elena Feld.

clypeus two symmetrical red marks similar to those present in certain specimens of *trinidadensis*, *hyalina*, and *recurva*. The labrum somewhat variable: sometimes black, in other cases red. The scape usually with a longitudinal brownish streak in front, more rarely entirely dark (certain specimens from Peru); the flagellum usually dark above, more or less brownish below; the antennal sockets brown.

THORAX: Black to sometimes more or less brownish (especially on the sides), of somewhat subdued sheen on mesonotum and scutellum due to the usually grayish tomentum (in some lights brownish) over these areas; the tomentum on the pleura and the sides of the propodeum usually silvery gray. The erect simple hairs black, their distribution and relative length as indicated in the description of the subgenus *Trigona*.

LEGS: Somewhat variable in color, the hind

pair and also the front and middle pair frequently brownish, although in other cases (especially specimens from Rio Colorado, Bolivia) the legs are predominantly black to the inclusion of the tarsal joints. Many of the specimens with brown legs have other earmarks of the callow; on the other hand, there are individuals that in all other respects except the legs are dark colored. The hind tibiae (fig. 17) gradually but not very strongly widened from base to apex, with their apical contour uniformly or nearly uniformly rounded, not partly emarginate or definitely angulate posteriorly as in so many other species of the subgenus *Trigona*; the outer face of the joint gently arched, at least anteriorly, over most of its extent, rather briefly flattened posteriorly towards the apex; the comb anteriorly at the apex of the hind tibiae somewhat feebly developed. The flat area margining the under side of the hind tibiae posteriorly is relatively narrow; at its widest near the apex it is somewhat less than one-third the width of the joint. The hind metatarsi as a rule approximating the hind tibiae in width, about four-fifths as wide at their widest (near the apex) as the hind tibiae are wide at their widest, but sometimes no more than two-thirds as wide (specimens from Tukeit, British Guiana); the hind metatarsi subparallel sided, a little contracted at the base, their apex posteriorly slightly produced downward, forming an acute angle. The hairs of the legs predominantly black, but with the following relatively minor exceptions: the hairs of the fore trochanters beneath usually pale; the plumose hairs intermixed with the erect black hairs on the outer face of the middle tibiae grayish or brownish rather than black (these plumose hairs are not so constant as in some of the other species of the subgenus *Trigona*; indeed they are often only sparsely present or even entirely absent from the middle tibiae); the microscopic erect hairs on the elevated part of the under side of the hind tibiae and adjacent apical part beneath of the associated femora silvery gray; the sub-oval sericeous patch at the base of the inner face of the hind metatarsi silvery gray or even whitish (sometimes the hairs are rubbed off or so changed in coloration by adherent sticky material that the silvery gray or whitish sheen is lost); the

metatarsal brushes black to copper colored. The relative length of the hairs and their distribution as noted in the description of the worker of the subgenus *Trigona*. The spines along the inner margin of the hind tibiae close to the apex very short, not visible ordinarily if the leg is viewed from the outer side and held level.

WINGS: Subhyaline, more transparent than those of *amalihea*, with their basal part barely or not at all darker than the apical part of the wing. The venation and stigma light brownish to sometimes more or less fuscous, especially in the case of the costal and subcostal veins. The transverse cubital veins sometimes moderately defined, in other cases very obscure to absent. The first discoidal cell more than eight-tenths as long as the marginal cell. The number of hamuli on each hind wing usually five, sometimes six or even seven. Of 244 wings examined, 208 had five hamuli, 33 had six hamuli, and three had seven hamuli, an average of 5.12. The tegulae black to dark brown.

ABDOMEN: Black or, rather more frequently, dark brownish, in many cases not telescoped, subequal to or narrower than the thorax, trigonate. The hairs black. Tergites 2 and 3 with a narrow band of microscopic tessellation along the apex, corresponding with the presence of appressed or semi-appressed hairs. Tergites 4 and 5 also sometimes with feeble traces of tessellation along the apex and scant appressed hairs in this area but in addition with longer erect hairs over approximately their apical half. Tergite 6 rather more extensively covered with erect hairs. A low growth of sericeous hairs, silvery gray in some lights, on each side of the middle of sternites 3 to 5 and over sternite 6. When the abdomen is telescoped, the hair bands of the venter usually form a continuously hairy surface.

MEASUREMENTS: Length 4 to 6.25 mm.¹; width of thorax 1.75 to 2 mm.; length of fore-

wing, including tegula, usually about 5.75 mm.

QUEEN

Unknown.

MALE

Unknown.

TYPE MATERIAL

The specimens on which Silvestri's description was based were obtained from a subterranean nest in Coxipò, near Cuyabá, in the Brazilian State of Matto Grosso. Two cotypes are in the American Museum of Natural History.

DISCUSSION

Trigona hypogea and its variety *robustior* are as a rule readily separable from their close relatives of the subgenus *Trigona* by the shape of the hind tibiae, which in the worker are narrow (especially so in the typical form), only very gradually widened towards the apex, and with the apical contour almost always rounded instead of angulate or distinctly truncate. The contour of the hind tibiae of this caste is a little suggestive of that of a baseball bat in the gradual and symmetrical expansion from base to apex. Like the worker of *amalihea* the present species and its variety *robustior* have a notably flattened clypeus, which in many instances (callows) is more or less mahogany stained.

In the American Museum of Natural History are specimens from several localities that Friese has designated *Trigona argentata*. If Friese's conception is correct, *hypogea* is merely a synonym of *argentata*. The type of *argentata* no longer exists, and in its absence it would seem unsafe to attempt to apply the brief description of Lepeletier, especially as that description is based upon an insect of unknown country. Yet such characters as the silvery pile of the face and transparent wings (noted in the description of *argentata*) almost tempt one to think that Friese may be right. If only Lepeletier had supplemented his description with mention of a few structural characters or if only the type were in existence! Schulz (1904b, p. 827) alluded to certain specimens collected by Bates along the Amazon that Friese interpreted as *argentata* and compares them with a series in his

¹ Silvestri (1902b, p. 133) gives 6.5 mm. as the length of *hypogea*. Among the present specimens only a few attain a length of as much as 6.25 mm., and then only due to rather exceptional distension of the abdomen. Most of the other specimens range between 4 and 5.5 mm., and two cotypes of *hypogea* which Professor Silvestri kindly presented to the American Museum measure between 4 and 5 mm.

own collection that Michaelis had obtained in Dutch Guiana. "The latter," according to Schulz, "appear to be somewhat larger and more robust (up to 6.5 mm. in length) and with relatively narrower hind tibiae than the Amazon specimens." Diversity of size is characteristic of *hypogaea*, but relative narrowness of the tibiae in large specimens (variety *robustior*) does not accord with the condition of the specimens in the collections here reported upon.

While Friese interpreted *argentata* as an insect structurally and in other respects like *hypogaea*, Ducke, on the other hand, made *argentata* an insect structurally equivalent to *fulviventris*, which he regarded as no more than an aberration of *argentata*.¹ In the Latreille collection at Oxford University there is an insect labeled *argentata*. The handwriting is that which Westwood has asserted to be the handwriting of Latreille. The insect in question is totally different from either *hypogaea* or the black-bellied form of *fulviventris*, being indeed no other than the light-colored extreme of Lepeletier's *quadripunctata*.

When students of the Meliponidae differ so widely in their interpretations of *argentata*,

¹ This, at least, is the stand taken by Ducke in his later papers (1916, pp. 123-129; 1925, pp. 416-417; 1945, p. 97). Prior thereto (1902b, p. 313) he had expressed the opinion that, although *argentata* is to be distinguished from *fulviventris* "almost solely through its darker abdomen," it is nevertheless "certainly distinct from it specifically, as it differs from it in its habits of life. The species considered (*argentata*) is rarely found at flowers, usually at rotting substances, excrement, and the like. In the Goeldi Museum I collected the species frequently in numbers at the flesh of animals that were being prepared for exhibition. In the immediate vicinity of the department of preparation there were a number of banana plants constantly bearing more or less bloom; never have I seen so much as a single *argentata* visiting these whereas *fulviventris* frequents them in numbers. The latter, on the other hand, I have never observed at meat."

Such a contrast in habits between two insects structurally identical would indeed be singular if proved to be constant. The fact that *argentata*, as interpreted by Friese, is partial to decaying meat makes one wonder whether after all Ducke had that insect before him rather than *guianae* (the dark variety of *fulviventris*) when he drew comparison with *fulviventris*. One thing is certain: that *hypogaea* is an insect structurally very different from either *fulviventris* or its dark form *guianae* as interpreted in the present paper, and Ducke's decision to regard both *fulviventris* and *hypogaea* merely as aberrations of *argentata* is accordingly puzzling.

it seems wiser to give recognition to the name *hypogaea* for the insect here considered.

To small specimens of *Trigona hypogaea*, Friese gave the name (apparently only a manuscript name) of *argentata minor*.

Silvestri (1902b, p. 133) collected the type specimens of *hypogaea* from a subterranean nest located at a depth in the earth of 30 cm. The nest entrance did not protrude above the surface of the soil, but took the form of an oval hole about 5 mm. wide, lined with wax. Within at the left were the combs and at the right the receptacles for honey and for pollen. The entire nest measured 26 cm. in length by 12 cm. in height.

In contrast to the aggressive behavior of some members of the subgenus *Trigona* the present species was reported by Silvestri to be "completely innocuous," failing even to attack anyone pillaging its nest.

The honey Silvestri pronounced rather dense, limpid, and sweet.

Like many other stingless bees this species is attracted by the carcasses of dead animals. Under the name *recurva* there appears the following notation regarding *hypogaea* based on a field note by Lutz: "Tukeit; July 17 and 21. A snake had been killed and skinned the 15th. *Trigona recurva* (*hypogaea*) was very abundant at the carcass on the 16th and, on the 17th, both *Trigona pallida* and *Melipona interrupta oblitescens* were collected there. Apparently they not only sucked the fluids but also carried off small bits of the flesh" (cited by Cockerell, 1920c, p. 460).

Later in the same publication (p. 464) Cockerell again cited Lutz as follows: "Kaie-teur; both in the forest and on that part of the open savannah where there was either bare rock or very few grasses and small, low flowers; July 30 to August 5; some of those from the forest were at the carcass of a dead monkey and others at fleshy flowers which had fallen to the ground from the high trees along the river."

DISTRIBUTION

The species was described from Coxipò, in Matto Grosso. The material before me includes specimens of *hypogaea* from the following countries, to which should be added Colombia if *argentata*, as interpreted by

Kriechbaumer (1900, p. 99), may be assigned to *hypogea*:

BRITISH GUIANA: Tumatumari, July 11, 1911 (F. E. Lutz); Tukeit, July 16, 1911 (F. E. Lutz), at the carcass of a snake; Kaieteur, July 30, 1911 (F. E. Lutz); Demerara River, March 8, 1913; Kartabo, Aug. 9, 1920 (W. M. Wheeler); Sept. 26, 1922 (W. Beebe), July 20, 1924 (J. F. W. Pearson); Kamakusa, Jan., 1923 (H. Lang).

SURINAM: Locality not indicated.

PERU: El Campamento, Colony of the Perené, June 18, 1920; La Chorrera to La Sombra, Aug. 21, 1920; La Sombra, Aug. 22, 1920 (Cornell Univ. Exped.).

BOLIVIA: Río Colorado, Sept. (W. M. Mann); Rurrenabaque, Río Beni, Dec. (W. M. Mann); Río Negro, Jan. (W. M. Mann).

BRAZIL: State of Matto Grosso: Coxipó, near Cuyabá (Silvestri), cotypes.

Trigona (Trigona) hypogea variety robustior Schwarz

Trigona (Trigona) hypogea variety *robustior* SCHWARZ, 1940, pp. 2-3.

Trigona hypogea robustior, MOURE, 1944a, p. 73.

WORKER

Structurally like typical *hypogea* but differs by its more robust appearance and its greater wing length.

MEASUREMENTS: Width of head 2.5 mm. as against 2 mm. for the typical variety; width of thorax about 2.25 mm. as against 1.75 to 2 mm. for the typical variety; length of forewing, including tegula, about 6.75 mm. as against about 5.75 mm. in the typical variety (see footnote to description, p. 231, of typical *hypogea*). Number of hamuli per lower wing ranges from four to six but is usually five. Of 84 wings examined, 66 had five hamuli, 16 had six hamuli, and two had four hamuli, an average of 5.17.

QUEEN

Unknown.

MALE

Unknown.

TYPE MATERIAL

The holotype was collected on the upper Essequibo River and is deposited, with paratypes, in the American Museum of Natural History. Other paratypes are in the United States National Museum, the Academy of

Natural Sciences of Philadelphia, and Cornell University.

DISCUSSION

This variety was separated from the typical variety with some diffidence, and earlier doubts regarding its distinctiveness have reasserted themselves, especially in view of the fact that occasional specimens are found (in particular a series from Tukeit, British Guiana) that are somewhat intermediate in size. In the main, however, the wing length and the other dimensions approach constancy in each of the forms, typical *hypogea* and variety *robustior*. The relationship between these forms is somewhat comparable to that between the Indo-Malayan *iridipennis* and its variety *valdezi*, in which size is the principal distinction. Indeed, one might go a step further and call attention to the fact that the worker of the Indo-Malayan *geissleri* is hardly to be separated from the worker of *iridipennis* and of *valdezi* except on the basis of size, representing as it does yet another gradation of stature. But what I interpret as the male of *geissleri* (Schwarz, 1939c, p. 117) is different from the male of *iridipennis* and until the male of *robustior* is known one cannot be certain whether that sex may not tend to confirm the separation of *robustior* from typical *hypogea*, which at present seems of possibly doubtful validity.

A very large number of the specimens here assigned to *robustior* seem to be callows, with instances where the entire body or large parts of it are mahogany colored rather than black. The series, including the holotype, from the upper Essequibo River embraces specimens that in all other respects seem to have passed completely out of the callow stage, with black or blackish head, thorax, legs, and abdomen; yet even these specimens retain the two mahogany spots on the clypeus that so often occur not only in *robustior* but also in the typical variety. These Essequibo River specimens have, in addition, the mandibles largely or wholly mahogany colored except for the blackish teeth. In respect to the coloration of the mandibles they are like specimens collected between La Chorrera and La Sombra and from La Chorrera itself in Peru; but other specimens (Colony of Perené, Peru, and particularly those from localities in Bolivia)

have the mandible colored much more nearly like that of *amalthaea*: black with a stripe of red just behind the toothed apical end. I have placed these specimens in *robustior* because of their virtual identity in size with that variety, although in the color of their mandibles they approximate the two cotypes before me of typical *hypogaea*. The Brazilian specimens show variability, some (even from the same locality) having the mainly blackish, others the mainly mahogany-colored, mandible. Probably the retention of red indicates an incomplete emergence from the callow state.

As in typical *hypogaea*, these larger insects of identical structure are partial to carrion.

DISTRIBUTION

The distribution of the variety *robustior* interdigitates with, and in other cases coincides with or overlaps, that of the typical variety. The type material included representatives from the following localities:

BRITISH GUIANA: Upper Essequibo River, Dec. 23, 1937 (W. G. Hassler), including holotype; Moraballi Creek, Essequibo River, Aug. 13, 1929, and Sept. 5, 1929, some of the specimens taken on carrion (Oxford Univ. Exped.).

ECUADOR: Mera, Feb., 1923 (F. X. Williams).

PERU: Colony of the Perené, June 5, 1920 (Cornell Univ. Exped.); El Campamento, June 22-26, 1920 (Cornell Univ. Exped.); San Antonio del Río Cotuhé. Putumayo District: La Chorrera, Aug. 17-20, 1920 (Cornell Univ. Exped.); La Chorrera to La Sombra, Aug. 21, 1920 (Cornell Univ. Exped.); El Encanto, Aug. 25, 1920 (Cornell Univ. Exped.).

BOLIVIA: Huachi, Río Beni, Aug. (W. M. Mann); San Fernando Rapids, Aug. (W. M. Mann); Santa Elena, Aug. (W. M. Mann); Covendo, Sept. (W. M. Mann).

BRAZIL: State of Amazonas: Pôrto Velho, Rio Madeira (Mann and Baker). State of Pará: Santarem (H. H. Smith). State of Matto Grosso: Chapada (probably Sant'Anna do Chapada, near Cuyabá), (H. H. Smith).

Trigona (Trigona) hyalinata variety *hyalinata* (Lepeletier)

Melipona atratula ILLIGER, 1806, p. 158 (without description).

Melipona? (*Trigona*) *hyalinata* LEPELETIER, 1836, p. 428.

Trigona hyalina, SPINOLA, 1840, p. 124 (identified by J. C. F. Klug).

Trigona hyalina, ERICHSON, 1841, p. 219.

Melipona hyalina, DALLA TORRE, 1896, p. 579.

Trigona flavipennis FRIESE, 1900a, p. 385.

Trigona hyalinata, SILVESTRI, 1902b, pp. 137-138.

Trigona flavipennis, H. VON IHERING, 1904b, p. 386.

Melipona ruficrus subspecies *flavidipennis* DUCKE, 1916, opposite p. 28, p. 133.

Melipona ruficrus subspecies *flavidipennis*, DUCKE, 1925, pp. 344, 421.

Trigona hyalinata, SCHWARZ, 1932a, p. 434.

Trigona ruficrus flavidipennis, R. VON IHERING, 1940, p. 403.

Trigona hyalinata, MOURE, 1944a, p. 73.

Melipona ruficrus subspecies *flavidipennis*, DUCKE, 1945, pp. 100-101.

WORKER

DIAGNOSTIC CHARACTERS: Black. Mandible five toothed, reddish or reddish brown over most of its surface. Length of malar space about equal to width of flagellum. Clypeus gently arched, its surface rather smooth and even, its greatest width fully twice as great as its length. Short, erect, black hairs on clypeus and supraclypeus, also on scape. Hind tibiae with a well-defined and somewhat inwardly placed angle at the apex posteriorly. Wings hyaline to often rather pronouncedly milky.

HEAD: Black or mainly black. The facial quadrangle wide, the distance between the compound eyes at a level just below the middle ocellus about equal to the distance from the middle ocellus to the apex of the clypeus. The compound eyes rather strongly convergent below, the distance that separates them at their level of greatest approximation (below) being about as 7.5 is to 9 when compared to their divergence at the level just below the middle ocellus. The clypeus raised a little above the level of the sides of the face, gently arched, its surface rather smooth and even, unfurrowed down the middle although sometimes a little flattened in this region, and not foveate or barely subfoveate at the middle of the apex. The length of the clypeus about one-half that of its greatest width; its anterolateral extremities separated from the compound eye by about the width of the flagellum. The supraclypeus prominent. The labrum simple. The mandibles (fig. 18) armed with five teeth. The length of the malar space at its middle about equal to the width of the

flagellum. The distance separating each lateral ocellus from the other approximately the same as that between a lateral ocellus and the nearest compound eye. Carina behind ocelli moderately developed and somewhat blunt. The clypeus, front, vertex, and lower one-third of the genal area more or less moderately shiny. The sides of the face, the upper two-thirds of the genal area, and to a slightly less extent the front and the clypeus with the usual appressed microscopic silvery gray hairs (see comments, however, on specimens from State of Goyaz in discussion, p. 238). The erect hairs black except for the rather long hairs on the lower edge of the mandibles, which range from black to copper colored. The short, erect, black hairs on clypeus and supraclypeus rather abundant, a little shorter usually than those at least along the inner face of the scape but longer than those on the lower part of the front, which, however, are soon succeeded by hairs of much greater length upward towards the vertex. The mandibles mostly red or reddish brown, with merely the basal prominences and the teeth along the apical edge black. The clypeus usually black as is the rest of the head but sometimes with two symmetrical red marks (a relic probably of the callow stage). The antennal sockets brown. The flagellum dark above, usually brown beneath; the scape with a usually pale brown, longitudinal streak in front.



FIG. 18. Mandible of worker of *Trigona (Trigona) hyalinata* variety *hyalinata* (Lepeletier). Drawing by Alice Gray.

THORAX: Black, of somewhat subdued sheen due to the presence of the somewhat dull gray to more or less brownish tomentum on the mesonotum, scutellum, pleura, and sides of propodeum in addition to the longer, more conspicuous, but sparser simple black hairs in these areas. The relative length of the hairs as indicated in the description of the subgenus *Trigona*.

LEGS: Usually black but sometimes dark brownish or invaded by brownish, especially in the case of the hind pair, and the apical joint of the tarsi usually touched with ferruginous. The hind tibiae (fig. 19) clavate in outline, much wider at the apex than at the

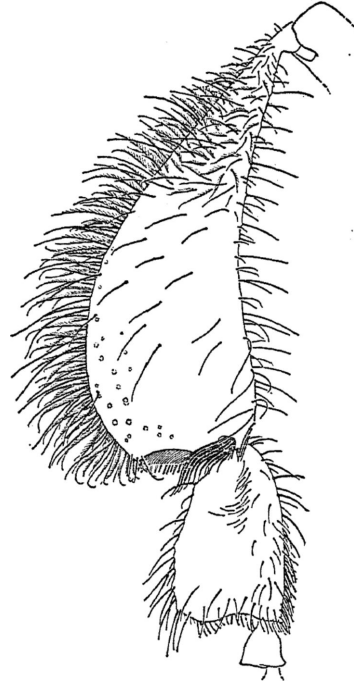


FIG. 19. Hind tibia and metatarsus of worker of *Trigona (Trigona) hyalinata* variety *hyalinata* (Lepeletier). Drawing by Alice Gray.

base, their anterior lateral contour gently emarginate, their posterior lateral contour strongly convex; their apex with an inconspicuous angle anteriorly that bears the comb, followed by a curvilinear bulge in the contour, which in turn is succeeded by an emargination that ends in a well-defined and somewhat inwardly placed angle where the apical contour meets the posterior contour; the outer face of the hind tibiae so gently arched as to approximate a flattened condition over its basal two-thirds but more decidedly flattened to slightly excavated over approximately the apical one-third. The flattened area margining the under side of the hind tibiae posteriorly about one-third the width of the joint near the apex. The hind metatarsi nearly three-fourths as wide at their

widest (near the apex) as the hind tibiae are wide at their widest, their posterior apical angle not strongly developed, somewhat rounded and approximating the rectangular rather than the acute. The hairs of the legs predominantly black but with the following relatively minor exceptions: sometimes the shorter hairs on the under side of the fore trochanters tend to be pale; the plumose hairs that are abundantly intermixed with the black simple hairs on the external face of the middle tibiae and frequently also on the basal part of the external face of the middle metatarsi are sometimes deep grayish brown rather than black; the microscopic but stubby hairs on the elevated part of the under side of the hind tibiae and adjacent apical part beneath of the hind femora are silvery gray; the sub-oval sericeous patch at the base of the under side of the hind metatarsi is silvery gray when not discolored by foreign material; the metatarsal brushes black to copper colored. The relative length of the hairs and their distribution as indicated in the description of the worker of the subgenus *Trigona*.

WINGS: Hyaline to often rather pronouncedly milky, with a whitish transparency. The nervures and stigma bright ferruginous to the inclusion of the costal and subcostal veins. The median cell not perceptibly darker than the other cells. The transverse cubital veins virtually obsolete, traceable only, if at all, as watery streaks. First discoidal cell about three-fourths as long as the marginal cell. The marginal vein sometimes with a tendency to fade out towards its apical extremity. Number of hamuli on each lower wing usually five or six, very rarely four or seven. Of 125 wings examined, 71 had five hamuli, 50 had six hamuli, two had four hamuli, and two had seven hamuli, an average of 5.42.

ABDOMEN: Black, usually telescoped and fairly compact, comparable in width with the thorax, devoid of punctures except for a few small scattered ones on tergites 1 and 2 of some of the specimens. Black are the narrow apical band of appressed hairs on tergite 2 and the more erect hairs apically on tergite 3, on the apical half of tergites 4 and 5, and on tergite 6, but in addition tergite 6 frequently has a covering of dull gray tomentum. The apex of tergite 2 and usually also tergite 3 covered very narrowly with feeble micro-

scopic tessellation coextensive with the hair bands. The under side of the abdomen likewise with erect black hairs along the apical half of the sternites and with dark inconspicuous tomentum as well on each side of at least sternites 3 to 5; the tomentum of sternite 6 tends often to be lighter in hue and the longer black hairs are few to absent. The hairs of the venter like those of the upper side often seem continuous owing to the usual telescoping of the abdomen.

MEASUREMENTS: Length 5 to 6.5 mm.; width of thorax 2.5 to 2.75 mm.; length of forewing, including tegula, 7.25 to 7.5 mm.

QUEEN

Unknown.

MALE

Unknown (see description of male of variety *branneri*).

TYPE MATERIAL

Trigona hyalinata was described by Lepeletier from São Paulo, Brazil. Two insects of different character (see discussion) bear the type label and the designation *hyalinata* in the Muséum d'Histoire Naturelle in Paris. It is possible that they were both originally included in the type material, but it is also possible that, as with so many other alleged types of Lepeletier, they are both spurious. Lepeletier himself adds somewhat to the mystery by saying in a footnote (p. 428) to his description of 1836 that, "Having described this species many years ago, I doubt today whether it belongs to this genus." However, the overwhelming likelihood is that this allusion is not to a published description but to a description held in manuscript, as were so many of the other descriptions of Lepeletier, until it could be finally published in 1836. Even so far back as 1825, Lepeletier stated (1825, p. 710) that he then had descriptions of nearly 40 meliponid species in an unpublished monograph of the bees. This number approximates that of the meliponids, 36 in all, of which Lepeletier published descriptions in 1836.

DISCUSSION

As I have previously pointed out (1938, p. 458) there are two different insects, both labeled type of *hyalinata* and both from the

"Capitainerie de St. Paul" (from which *hyalinata* was described), in the Lepeletier collection in the Muséum d'Histoire Naturelle in Paris. Both are in a poor state of preservation, cluttered with foreign material, so that their characters are badly obscured. One of them seems to be the insect that Friese named *subterranea*, which is structurally identical with Smith's *mombuca* and therefore to be considered merely a variety of *mombuca*. The other, in so far as its characters are traceable, is structurally like *hyalinata* as interpreted by Friese and Ducke.

Nowhere in Lepeletier's brief description of *hyalinata*, based on the worker, did he allude to the hairs as black, which is predominantly the condition of the hairs in what Friese and Ducke have designated *hyalinata*. The hairs of the face Lepeletier speaks of as "recumbent" and "of white color." This well applies to *subterranea* but, on the other hand, is at least not un-descriptive of the pale appressed pile on the sides of the face of *hyalinata* as interpreted by Friese and Ducke, although black hairs predominate on the face. "Cinereous," as applied to the hairs of the thorax, legs, and abdomen, is more in accord with the condition of *subterranea* than with that of the rival claimant, and in point of size, too, *subterranea* more nearly answers the specification "a little smaller than *ruficrus*" than does the *hyalinata* of the Friese-Ducke interpretation. Indeed Ducke (1916, p. 132; 1925, p. 420; 1945, p. 100) gives the identical measurements for *hyalinata* that he had previously given for *ruficrus* (1916, p. 130; 1925, p. 418; 1945, p. 98). If the interpretation of Friese and Ducke had not resulted virtually in the establishment of a lectotype, I should have been inclined to select *subterranea* as the more eligible claimant to rank as *hyalinata*, but it does not seem desirable under the circumstances to upset the established nomenclature.

But even if the Friese-Ducke interpretation of *hyalinata* be adopted, as seems in view of the circumstances advisable, it should be emphasized that *hyalinata* consists of more than one variety and that Ducke, at least, has interpreted as typical *hyalinata* what is rather a northern race of *hyalinata*, namely, *hyalinata* variety *branneri* Cockerell. Typical *hyalinata* (from southern Brazil) is in my

estimation the same bee that Friese (1900a, p. 385) described as *flavipennis* and that Ducke (1916, p. 133; 1925, pp. 344, 421; 1945, pp. 100-101) subsequently named *flavidipennis*. Friese's *flavipennis* was obtained from the same region (São Paulo) as Lepeletier's *hyalinata*, and Friese in his identifications has labeled (at times as *hyalinata*, at other times as *flavipennis*) specimens that seem to me to be one and the same thing. On the other hand, Ducke considered as typical *hyalinata* the form here designated *hyalinata* variety *branneri* in which, while the apical part of the wing is whitish transparent, the basal part (more particularly the median cell) is somewhat brownish. Two factors militate against the correctness of Ducke's interpretation. In the first place, the somewhat darkened median cell is characteristic of the insects (variety *branneri*) in the northern part of the range of *hyalinata*, but, so far as the specimens before me justify a conclusion, it is not characteristic of the insects of the more southern part of the range.¹ In the second place, Lepeletier's description of *hyalinata* very definitely states "Wings hyaline, with testaceous nervures." It seems hardly likely that Lepeletier would have applied the name *hyalinata* to an insect that by the darker staining of its wings belied that designation.

Silvestri (1902b, p. 138) was inclined to make *hyalinata* a subspecies of *ruficrus*,² and Ducke (1916, p. 132; 1925, p. 420; 1945, p. 100) actually so subordinated it. The two insects, however, are structurally different, for the *ruficrus* worker has a rather conspicuous longitudinal channel down the middle of its clypeus that gives the region on each side of

¹ Ducke (1916, p. 132; 1925, p. 420) gives, it is true, locality records for the northern race (*hyalinata* variety *branneri*) that include places in such southern Brazilian states as Rio de Janeiro and São Paulo. He indicates, however, that "in Amazonia this (as all other) subspecies are well distinguished while in the south they tend in many instances to merge into the subspecies *fuscipennis*." As *fuscipennis* (a synonym of what is in this paper interpreted as *amalthaea*) is structurally well differentiated from *hyalinata* it is hard to know just what is meant by this transition. In any event his comment would seem to cast some doubt on the propriety of including these more southern states in the range of the northern form of *hyalinata*.

² Silvestri states: "This species, *hyalinata*, is so closely related to *T. ruficrus* that it would be better to consider it a subspecies of the latter."

the channel a somewhat swollen appearance, whereas in the *hyalinata* worker the clypeus is of an approximately smooth, even, unfurrowed surface. Yet it must be confessed that, while the clypeus of *hyalinata* is easily distinguished from that of typical *ruficrus*, there are certain specimens of *corvina*, hitherto considered a variety of *ruficrus*, that tend to approximate in the structure of their clypeus the smooth condition characteristic of *hyalinata* and make it necessary to rely on other supplementary characters to separate the two. Usually the erect hairs on the clypeus of *hyalinata* are more developed than is the case in *corvina*, and the whitish transparency of the wings of typical *hyalinata* is especially to be relied upon in separating this form.

The series from an unspecified locality in the State of Goyaz, Brazil, assigned to *hyalinata* in this paper, is in several respects aberrant. In all of the specimens of this series the hair on the clypeus is either sparse or absent, in some the front is hairless, while in one instance half of the front is bare and shiny, the other half densely covered with hair. The specimens are unusual, furthermore, in having in many instances no hairs on the scape, in other instances a downy condition resembling that of *amalihea*. The majority of these specimens have extensive bare patches on the mesonotum and on the scutellum. In other respects these specimens are, however, so like *hyalinata* that I hesitate to separate them from it, especially in view of the instability they show from specimen to specimen. It would seem likely that the hairs were artificially removed for purposes of study by an earlier worker.

Silvestri (1902b, p. 138) noted that the nests of *hyalinata*, as are those of *ruficrus*, are built in the open, being placed on a wall or on the limb of a tree instead of within a hollow trunk. The nests were not accessible to him but, viewed from a distance of 4 meters, the external form seemed different from that of the nest of *ruficrus*. Cone shaped and with an irregular protuberance at the side, the nest of *hyalinata* was about 50 cm. in height. The entrance appeared to the observer to be situated at the apex of the cone.

Silvestri rated *hyalinata* as no less aggressive than *ruficrus*.

Rodolpho von Ihering (1940, p. 403)

quoted A. Miranda-Ribeiro to the effect that in the State of Matto Grosso, Brazil, the common name for this bee is "guaxupé." On the other hand, Silvestri (1902b, p. 137) indicated that at Coxipó the name for this reputedly aggressive bee is "abelha brava," a designation it shares with *amalihea*.

DISTRIBUTION

Ducke (1925, p. 421) in discussing the range of Friese's *flavipennis* (*flavidipennis* Ducke), here considered a synonym of typical *hyalinata*, indicated that this form occupied "the southern parts of central Brazil and contiguous regions." He listed localities in the Brazilian States of Minas Gerais and São Paulo as well as in Paraguay and also included in the range the State of Goyaz without citation of locality. The westward extension of the form is, however, greater than Ducke supposed, for I have before me specimens not only from the Brazilian states he mentioned but also from the State of Matto Grosso, and even from Bolivia, Peru, and Ecuador. The specimens are from the following localities:

BRAZIL: State of Minas Gerais: Uberaba, 1900 (Draenert); Bello Horizonte, Nov. 1-6, 1919 (Cornell Univ. Exped.); Lassance, Nov. 9-19, 1919 (Cornell Univ. Exped.). State of Goyaz: Without locality designation. State of São Paulo: Jundiahy, 1897; São Paulo (Hammar); Franca; Arandandara. State of Matto Grosso: Miranda; Chapada (probably Sant' Anna do Chapada near Cuyabá), June-Aug. (H. H. Smith); Cicade Branco, Pôrto Velho, Aug. 20, 1943 (Mark Taylor).

BOLIVIA: Riberalta, Río Beni, Jan. (W. M. Mann); Cavinás, Río Beni, Feb. (W. M. Mann).

PERU: Iquitos, Aug. 1, 1920 (Cornell Univ. Exped.).

ECUADOR: Tena, March 5, 1923.

Trigona (*Trigona*) *hyalinata* variety *branneri* Cockerell

Melipona hyalinata, DUCKE, 1902a, pp. 325, 326.

Melipona (*Trigona*) *hyalinata*, DUCKE, 1902b, pp. 292, 314.

Trigona hyalinata, SCHULZ, 1904b, p. 827.

Trigona hyalinata, DUCKE, 1907, p. 89.

Trigona amalihea, MARIANNO, 1911, p. 79 (*ex parte*, according to A. Ducke, 1925, p. 420).

Trigona hyalinata, MARIANNO, 1911, pp. 8, 97, 107.

Trigona branneri COCKERELL, 1912b, p. 50,
Melipona ruficrus subspecies *hyalinata*, DUCKE,
 1916, pp. 15, 132.

Trigona ruficrus corvina, COCKERELL, 1920c, p.
 465 (record from Tumatumari, British Guiana,
 only).

Melipona ruficrus subspecies *hyalinata*, DUCKE,
 1925, pp. 344, 420.

Melipona ruficrus subspecies *hyalinata*, ALFKEN,
 1930b, p. 10.

Trigona (Trigona) hyalinata, SCHWARZ, 1938,
 pp. 438, 443, 457-459.

Trigona (Trigona) hyalinata variety *branneri*,
 FLEMING, 1945, p. 267 (identified by H. F.
 Schwarz).

Melipona ruficrus subspecies *hyalinata*, DUCKE,
 1945, pp. 99-100.

WORKER

As in *hyalinata* variety *hyalinata* except for
 the coloration of the wings.

WINGS: Basally somewhat darkened, particularly in the median cell; the costal and subcostal veins fuscous as well as often the other veins enclosing the median cell, but the stigma and veins in the rest of the wing rather bright ferruginous and the cells apical of the median cell clear to slightly milky. The tegulae dark rufo-fuscous to black. The transverse cubital veins very feebly indicated to absent. The first discoidal cell about three-fourths as long as the marginal cell. The apex of the marginal vein usually failing quite to reach the edge of the wing. Number of hamuli usually five, more rarely six. Of 118 wings examined, 109 had five hamuli, and only nine had six hamuli, an average of 5.07.

QUEEN

Unknown.

MALE¹

HEAD: Black. The facial quadrangle narrower than in the worker. The distance from one eye to the other at their level of closest approximation (below) about three-fourths the length of the eye, whereas in the worker the shortest distance between the eyes is about the same as the length of the eye. The distance between the eyes at the level just below the middle ocellus slightly less than the distance from the middle ocellus to the apex of the clypeus, about as eight is to nine. The

clypeus raised a little above the sides of the face, very gently arched and of a smooth, even surface, unfurrowed down the middle, and not foveate apically at the middle, its apico-lateral angles acute and narrowly but distinctly separated from the rim of the eye (by a distance approximating the width of the tip of the narrowed apical joint of the attenuated flagellum). The length of the clypeus about three-fifths its width. The supraclypeus prominent, triangular, about as long as it is wide at the base. The labrum simple. The mandibles without clear evidence of dentition along their inwardly receding apical edge; the base black but the apical one-half of the mandibles red except for the narrowly darkened apical edge. The malar space at its shortest part a little shorter than the narrow apical joint of the flagellum is wide. The distance between the lateral ocelli distinctly greater than that which separates a lateral ocellus from the nearest compound eye. A blunt low carina behind the ocelli. The head with longer erect black hairs than is the case in the worker, and particularly is this true as applied to the lower half of the face. The black hairs on the clypeus, particularly those on the apical half of the clypeus, and those on the labrum, fully as long as those towards the top of the front and longer than the hairs on the supraclypeus or those on the scape, which are about as long as the scape is wide. The black hairs of the vertex still longer than those of the clypeus and front, as are the black hairs fringing the inferior margin of the mandibles. Silvery gray microscopic appressed hairs rather dense over the clypeus, sides of face, and front, and especially so over the upper two-thirds of the genal area; the lower one-third of the genal area bare except for the erect hairs, which are black. The antennal sockets, the scape in front, and the flagellum below ferruginous.

THORAX: Black, of slightly subdued sheen due to the presence of dull gray to more or less brownish tomentum on the mesonotum, pleura, and sides of propodeum in addition to the longer, more conspicuous but sparser simple black hairs in these areas.

LEGS: Brownish black to black. The anterior lateral contour of the hind tibiae somewhat concave, their posterior lateral contour strongly convex, their apical contour rather

¹ Description based on a single specimen from Tumatumari, British Guiana.

evenly rounded, their greatest width (near the apex) about four-fifths that of the co-specific worker at the corresponding level. The hind metatarsi towards the apex about three-fourths the width of their tibiae, their exterior face rather swollen anteriorly, their apex posteriorly without angulation, rounded. The hairs of the legs predominantly black to blackish with the following relatively minor exceptions: the tomentum on the under side

tive length approximately as indicated in the generalized description of the male of the subgenus *Trigona*.

WINGS: Like those of the worker of *branneri*, basally somewhat darkened, particularly in the median cell; the costal and subcostal veins fuscous as well as the other veins enclosing the median cell, but the stigma and veins in the rest of the forewing rather bright ferruginous and the cells apicad to the median

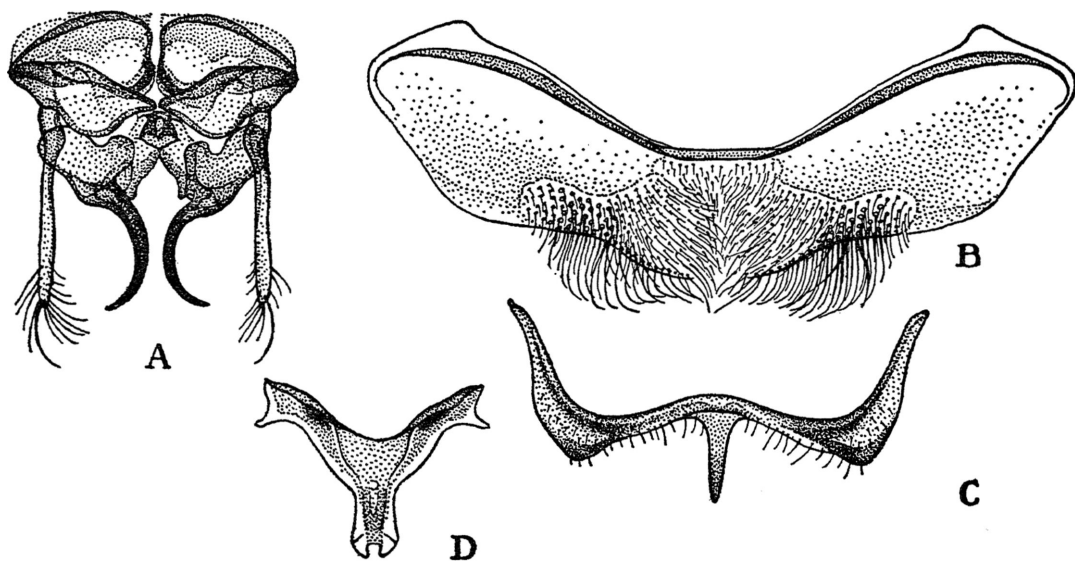


FIG. 20. Abdominal parts of the male of *Trigona* (*Trigona*) *hyalinata* variety *branneri* Cockerell. A. Genitalia (chitinized parts only). B. Sternite 5. C. Sternite 6. D. Sternite 7. All based on a specimen from Tumatumari, British Guiana. Drawings by Shirley H. Risser.

of the trochanters of the fore pair of legs, a fringe of very microscopic hairs on the under side of the fore and middle femora, the short bristles at the apex of the inner face of the hind femora, and the streak-like array of similar very short bristles narrowly down the elevated area of the inner face of the hind tibiae, as well as the sericeous flattened hairs at the base of the inner face of the hind metatarsi, all more or less silvery gray. The plumose hairs on the outer face of the middle tibiae abundant and the erect hairs of the legs long, the longer simple hairs of the mainly plumose fringe along the posterior lateral contour of the hind tibiae attaining a length that is fully two-thirds the greatest width of these tibiae. The distribution of the simple black hairs in general and their rela-

cell very slightly milky. Number of hamuli, in the only specimen before me, five in one lower wing and six in the other.

ABDOMEN: Black, about as wide as the thorax. The hairs of the tergites black: tergite 2 hairless except for a narrow apical band of appressed hairs and a few inconspicuous short hairs laterally; tergite 3 also largely hairless but with a few erect hairs in the narrow band of appressed hairs along its apex; tergites 4, 5, and 6 with progressively longer black hairs over their apical half. Tergite 7 narrowly brownish gray tomentose along its apex. The sericeous hairs of the sternites silvery gray. (Fig. 20.)

MEASUREMENTS: Length 5 mm.; width of thorax 2.5 mm.; length of forewing, including tegula, 7.25 mm.

TYPE MATERIAL

Described on the basis of eight workers from Manáos, Brazil. Holotype in the United States National Museum. A paratype in the American Museum of Natural History and a paratype also in the Museum of Comparative Zoölogy.

DISCUSSION

The form *branneri* is, in my estimation, incorrectly interpreted by Ducke as typical *hyalinata* (see discussion of *hyalinata* variety *hyalinata*, p. 237).

See also the discussion of *corvina* (p. 277) for certain convergences between that species and the present variety.

Specimens of *branneri* from Manáos, the type locality, and from Santarem have a little greater wing length than specimens from the other localities noted.

Ducke (1925, p. 420) reported that, so far as known, the nest of *branneri* is an exposed one, as distinguished from a concealed one.¹

Of the flowers visited by *branneri*, Ducke listed (1902a, p. 325; 1902b, p. 314) *Dichromena ciliata* Vahl, one of the Cyperaceae, as being outstandingly attractive. Also visited by this variety Ducke mentioned (1902a, p. 326) a species of the palm *Astrocaryum*.

In a letter accompanying a shipment of these bees from the State of Bolívar, Venezuela, Mr. Vincent A. Baker informed me that the popular name for *branneri* in the region in question is "pegon."

DISTRIBUTION

The range of this form, so far as the specimens before me indicate, is predominantly in the South American states bordering the Caribbean and southward into northern Brazil to the inclusion at least of the States of Amazonas and Pará. Ducke (1916, p. 132; 1925, p. 420; 1945, p. 100) made the range more inclusive, extending it southward to the fringes of the subtropics and embracing such Brazilian states as Maranhão, Bahia, Goyaz, Matto Grosso, Minas Gerais, Rio de Janeiro, and São Paulo, as well as the States of

Amazonas and Pará. He cited also a locality in Peru. However, Ducke indicated that south of the Amazon basin there is a tendency for *branneri* to lose its subspecific distinctness. If the more restricted range here indicated should prove valid, *branneri* occupies a territory intermediate between that of *corvina*, which, so far as known, does not cross from Central America into South America, and that of *ruficrus*, which has been reported from a number of the states in the eastern and southern part of Brazil as well as from Paraguay but is unknown from north central and northwestern Brazil and is probably absent from the South American states bordering the Caribbean and from all of Central America, notwithstanding one or two reports of its isolated occurrence in these areas (see distribution of *ruficrus* variety *ruficrus*, p. 270).

The specimens of *branneri* before me were collected at the following localities:

VENEZUELA: Mt. Duida region, Nov. 3 and Nov. 4, 1928 (G. H. H. Tate); Arabupu (Mt. Roraima region), 4400 feet, Nov. 24, 1938 (A. S. Pinkus); Caripito, March 3, 1942 (H. S. Fleming); San Felix, State of Bolívar, July 1, 1946 (V. A. Baker).

BRITISH GUIANA: Bartica, May 17, 1901; Kartabo, Aug. 5, 1920, Aug. 9, 1920, Aug. 31, 1920 (W. M. Wheeler), July 11, 1922, and Aug. 2, 1924 (J. F. W. Pearson); Penal Settlement, Bartica District, Oct. 7, 1920 (Cornell Univ. Exped.), April 8, 1929 (J. Ogilvie); Rupununi Cattle Trail between Essequibo and Demerara rivers, April-May, 1920 (G. B. Fox); Mary's Falls to Kaburi Rock, Mazaruni River, Aug. 17, 1920 (R. E. Wheeler); Amatuk, Feb. 16, 1921; Matope, July 23, 1924 (J. F. W. Pearson); Camaria, June 30, 1924 (J. F. W. Pearson); Tumatumari, June 11, 1911 (F. E. Lutz), without date (Leo E. Miller), June 29, 1927 (Cornell Univ. Exped.), May 31, 1929, male (J. Ogilvie); Monkey Jump, Essequibo River, Oct. 9, 1929, and Oct. 14, 1929 (Oxford Univ. Exped.); Waranama, Nov. 13-19, 1936 (J. Ogilvie).

SURINAM: Paramaribo, April 10, 1927; Sint Barbara Pln., Surinam River, April 12, 1927; Sanderij I., Boven, Para District, April 19, 1927; Moengo, Boven Cottica River, May 16, 1927; Kwakoegeon, Saramacca River, June 11, 1927, and June 13, 1927. (All of the Surinam specimens of 1927 were collected by the Cornell Univ. Exped.)

BRAZIL: State of Amazonas: Itacoatiara, Nov. 22, 1919 (H. Parish); Manáos (H. B. Merrill); Flores, Aug. 2, 1924; lower Rio Negro, Aug. 21,

¹ It is not clear whether Ducke's statement is based on observations made on *branneri* or whether he is applying to what is here separated as *branneri* the notations made by Silvestri (1902b, p. 138) on typical *hyalinata*.

1924; Vista Alegre, Rio Branco, Sept. 6, 1924. State of Pará: Pará, 1890 (Schulze), May, 1901 (A. Ducke); near Pará (H. B. Merrill); Santarem (H. H. Smith); Prata, June 30, 1919 (H. Parish).

Trigona (Trigona) hyalinata variety
amazonensis (Ducke)

Melipona ruficrus subspecies *amazonensis*
Ducke, 1916, pp. 132-133.

Melipona ruficrus subspecies *amazonensis*,
Ducke, 1925, pp. 344, 420.

Melipona ruficrus subspecies *amazonensis*,
Ducke, 1945, p. 100.

WORKER

As in typical *hyalinata* except for its somewhat greater size and the coloration of its wings.

WINGS: Of a uniform rather dull yellowish stain, of no deeper or scarcely deeper tinge in the median cell than in the cells more apically located and without a whitish transparency in these apically located cells. The venation and stigma ferruginous. The tegulae dark rufous to black. Transverse cubital veins very feebly indicated to virtually absent. The first discoidal cell about three-fourths as long as the marginal cell. The apex of the marginal vein usually just failing to attain the edge of the wing. Number of hamuli on each lower wing more often six than five. Of 136 wings examined 90 had six hamuli, and 46 had five hamuli, an average of 5.66.

MEASUREMENTS: Length 6.25 to 7.5 mm.; width of thorax 2.75 to 3 mm.; length of forewing, including tegula, 7.75 to 8 mm.

QUEEN

Unknown.

MALE

Unknown (see description of male of variety *branneri*).

TYPE MATERIAL

The type material of *amazonensis* is presumably in the Museu Paraense in Pará, Brazil. It included specimens from Teffé, State of Amazonas, and from Rio Acre in Acre Territorium, Brazil.

DISCUSSION

Ducke (1916, pp. 132-133; 1925, p. 420; 1945, p. 100) described *amazonensis* very briefly as follows: "Distinguished from the

other races [of *ruficrus*] by its greater size as well as by its almost uniformly yellow-stained wings,—a little darker at the base than at the apex. Length 7-7.5 mm., width of thorax 2.75 to 3 mm."

I have not had access to the type material of *amazonensis*, but I have specimens from Teffé, Brazil, one of the type localities, that so completely accord with Ducke's specifications and his systematic allocation of this form as to leave no doubt in my mind that the insects in question are *amazonensis*. The fact that Ducke makes *amazonensis* a subspecies of *ruficrus*, which has a clypeus different from that of the specimens under consideration, might seem to cast doubt on the accuracy of the present determination, but, on the other hand, Ducke has made several other *Trigona* subspecies of *ruficrus* in spite of the fact that their clypeus differs from that of *ruficrus* as sharply as does the clypeus of the insects here designated *amazonensis*. The linking by Ducke of *amazonensis* with *ruficrus* does not, therefore, of itself seem to militate against the present interpretation, and all of the other elements of his brief description support it.

Assuming that the present interpretation is correct, *amazonensis* is a variety of *hyalinata*, which it immediately follows in Ducke's numerical arrangement, rather than of *ruficrus*, to which Ducke subordinates not only *amazonensis* but likewise *hyalinata* as subspecies. The variety *amazonensis* shares the structural characters of typical *hyalinata* and differs from it only in the more yellowish, less transparent character of the wings, and in its somewhat larger size.

Ducke noted variability in size even in the limited material (confined to two localities) before him and stated that the smallest specimens approach in size the largest specimens of *hyalinata* (to be interpreted as *hyalinata* variety *branneri*), while the largest have a certain resemblance to a small *silvestriana* (the equivalent of what in the present paper is designated *trinidensis*). In the rather large series from diverse localities before me the body length varies, according to the extent to which the abdomen is telescoped, from 6.25 to 7.5 mm. On the other hand, the wing length, a far more trustworthy basis for measurement, is rather constant.

At San Luis de Shuaro, Valle de Chanchamayo, Weyrauch noted a nest (No. 147) of *amazonensis* that was located on a rock wall 6 meters high (pl. 5, fig. 4). The nest material was rose brown in color and the nest about 1 meter long.

On the other hand, a nest (No. 162) noted by Weyrauch at San Ramon was on a tree trunk.

Yet another notation by the same observer is of special interest: this bee was seen licking the fluids of Homoptera on an orange tree.

DISTRIBUTION

Ducke, when describing *amazonensis* (1916, pp. 132-133), had before him specimens only from Teffé and the upper Rio Purus, in the State of Amazonas, Brazil, and from Rio Acre in Acre Territorium.

The specimens here considered include one from the type locality, Teffé, collected on January 12, 1920, by H. Parish, and a single specimen also from Cicade Branco, Porto Velho, in the Brazilian State of Matto Grosso, collected August 20, 1943, by M. Taylor. All the others, preponderantly the more numerous, are from Ecuador, Bolivia, and Peru, as follows:

ECUADOR: Río Pastaza, March 19, 1939 (F. M. Brown).

BOLIVIA: Tarata, 1900; Santa Elena, Aug. (W. M. Mann); Covendo, Sept. (W. M. Mann); Huachi, Río Beni, Sept. (W. M. Mann); near mouth of Río Mapi, Sept. (W. M. Mann); Rurrenabaque, Río Beni, Oct. (W. M. Mann); Tumupasa, Dec. (W. M. Mann); Ixiamas, Dec. (W. M. Mann); Ivon, Río Beni, Feb. (W. M. Mann).

PERU: El Campamento, Colony of the Perené, June 19, 1920 (Cornell Univ. Exped.); Hda. San Juan, Colony of the Perené, June 23, 1920 (Cornell Univ. Exped.); lower Río Pachitea, July 22, 1920 (Cornell Univ. Exped.); El Encanto, Putumayo District, Aug. 26-27, 1920 (Cornell Univ. Exped.); middle Río Marañón, Nov. 5, 1925 (H. Bassler); San Ramon, Valle de Chanchamayo, 800 meters, 1939, No. 46, No. 147, and No. 162 (W. Weyrauch); San Luis de Shuaro, Valle de Chanchamayo, April 1, 1939, No. 61 (W. Weyrauch); Oxapampa, 1200 meters, 1940, No. 54 (W. Weyrauch); Tingo Maria, Río Huallaga, 700 meters, April 1, 1940, No. 74 (W. Weyrauch); Satipo, 600 meters, Aug. 10, 1940 (W. Weyrauch); Iquitos (H. Bassler).

Trigona (Trigona) trinidadensis variety *trinidadensis* (Provancher)

? *Apis Sylvestris* BARRÈRE, 1741, pp. 190-191.
? *Apis sylvestris*, FERMIN, 1769, pp. 300-301.
Apis amalthea, COQUEBERT, 1804, p. 97, pl. 22, fig. 4.

? *Apis sylvestris*, AZARA, 1809, p. 160.
? "Sanharo grosso," SPIX AND MARTIUS, 1828, p. 542.

Melipona (Trigona) amalthea, LEPELETIER, 1836, pp. 425-426, exclusive of description of nest.
Trigona amalthea, DRAPIER, 1845, p. 511.

"Sanhora," ANONYMOUS, 1878b, p. 74.
Melipona Trinidadensis PROVANCHER, 1888, pp. 344-345.

Melipona amalthea, PECKOLT, 1893, p. 580.
Melipona trinidadensis, DALLA TORRE, 1896, p. 584.

Trigona Amalthea, KRIECHBAUMER, 1900, p. 99.
Trigona amalthea, SILVESTRI, 1902b, pp. 143-144, pl. 1, fig. 19.

Trigona amalthea, H. VON IHERING, 1903, pp. 204, 239, 263, 277, pl. 10, fig. 2.

Trigona amalthea, H. VON IHERING, 1904b, pp. 381, 383, 386.

Trigona amalthea, GRÜNBERG, 1904, p. 14.
Trigona amalthea, SCHULZ, 1904b, p. 826.
Trigona amalthea, DUCKE, 1907, p. 90.

Trigona silvestriana VACHAL, 1908, pp. 221-222 (specimens from the State of Goyaz, Brazil; Bolivia; and Ecuador).

Trigona trinidadensis (= *Trigona amalthea*), FRIESE, 1909a, pp. 39, 40.

Trigona silvestriana, DUCKE, 1910a, p. 108.
Trigona amalthea, DUCKE, 1910b, p. 368.
Trigona amalthea, MARIANNO, 1910c, p. 8.

Trigona silvestriana, COCKERELL, 1912b, p. 61.
? *Trigona friesei* H. VON IHERING, 1912, p. 44.
Trigona amalthea, FRIESE, 1913, pp. 579-580.

Trigona amalthea, FRIESE, 1914b, p. 220.
Trigona silvestriana, SCHROTTKY, 1914, pp. 218-219.

Melipona silvestriana, DUCKE, 1916, pp. 15, 134-135, fig. 21.

Trigona amalthea, FRIESE, 1917, p. 299 (in part).
Trigona nigerrima, LUTZ AND COCKERELL, 1920, p. 499 (specimens from Río Charape, Peru, collected by Townsend in September¹).

Trigona amalthea, LUTZ, 1924a, pp. 205, 210, 216 (identified by H. Friese).

Trigona silvestriana, LUTZ, 1924a, p. 218.
Trigona silvestriana rohweri COCKERELL, 1925c, pp. 626-627.

¹ I have seen a specimen taken at Río Charape, Peru, by Townsend in September and it is, in my estimation, not *nigerrima* but *trinidadensis*.

- Melipona silvestriana*, DUCKE, 1925, pp. 344, 354, 421-422, pl. 4, fig. 21.
Trigona silvestriana, SALT, 1929, p. 444 (identified by H. F. Schwarz).
Melipona silvestriana, ALFKEN, 1930b, pp. 2, 10.
 ? *Trigona almalthea* (sic), MARTIN, 1930, p. 97.
Melipona silvestriana, ALFKEN, 1932b, p. 306.
Trigona amalthea, MAIDL, 1934, pp. 164, 316.
Trigona silvestriana, MAIDL, 1934, p. 576.
Trigona silvestriana, MYERS, 1935b, pp. 131-134.
Trigona (*Trigona*) *trinidensis* variety *trinidensis*, SCHWARZ, 1938, p. 438.
Trigona silvestriana, R. VON IHERING, 1940, pp. 705, 880.
Trigona (*Trigona*) *trinidensis* variety *trinidensis*, SCHWARZ, 1940, pp. 1, 3-4.
Trigona species, WEYRAUCH, 1942, pp. 62-64, fig. 6.
Trigona trinidensis, SOUKUP, 1943, p. 271.
Trigona trinidensis trinidensis, MOURE, 1944a, p. 73.
Melipona silvestriana, DUCKE, 1945, pp. 14, 101-102, pl. 7, fig. 21.
Trigona (*Trigona*) *trinidensis* variety *trinidensis*, FLEMING, 1945, p. 267 (identified by H. F. Schwarz).

WORKER

DIAGNOSTIC CHARACTERS: Black. Mandible five toothed, chestnut brown to reddish over most of its surface. Length of malar space greater than width of flagellum. Clypeus gently arched, foveate at the middle of the apex, otherwise generally of even surface although in some specimens with a faintly incised line down the middle. The width of the clypeus at its widest nearly three times as great as its length. Black erect hairs on clypeus, supraclypeus, and scape. The hairs over the front of rather uneven growth, somewhat coarse and ragged in appearance when the head is viewed in profile. Hind tibiae with a rather strong and somewhat inwardly placed angle at the apex posteriorly. Wings very dark and conspicuously long.

HEAD (FIG. 21A AND 21C): Black or predominantly black. The facial quadrangle wide, the distance between the compound eyes at the level just below the anterior ocellus about equal to the distance between the anterior ocellus and the apex of the clypeus. The compound eyes somewhat convergent below, the distance that separates them at their level of greatest approximation (below) being about as 11.75 is to 13 when

compared with their divergence at the level just below the anterior ocellus. The clypeus gently arched, rising somewhat above the sides of the face, foveate at the middle of the apex, otherwise generally of even surface, although in some specimens a faint incised line bisecting the clypeus longitudinally can be traced in certain lights. The width of the clypeus, measured from one apico-lateral extremity to the other, nearly three times its length; the apico-lateral extremities separated from the eye by about the width of the flagellum. The supraclypeus fairly prominent. The labrum simple (fig. 21A1). The mandibles armed with five teeth. The length of the malar space at its middle longer than (in large specimens nearly twice as long as) the flagellum is wide. The distance between the lateral ocelli only about two-thirds that which separates each lateral ocellus from the nearest compound eye. The carina behind the ocelli relatively well developed but somewhat blunt. Clypeus, front, vertex, and lower one-third of genal area more or less moderately shiny; the sides of the face dulled by a more or less dense covering of fine, appressed, microscopic silvery gray hairs; such hairs are sparsely present also on the clypeus and extend likewise to the front; the upper two-thirds of the genal area silvery gray pruinose. All the other hairs of the head erect, somewhat coarse, and black except that those fringing the lower border of the mandibles and the labrum are usually more copper colored. The black hairs on the clypeus, particularly those along the lower part of the clypeus to the inclusion of the anterolateral extensions, tend to be longer than the hairs on the supraclypeus and those on the scape, although they are shorter than the hairs of the labrum and shorter, too, than the hairs of at least the upper part of the front, which in turn are shorter than the coarse hairs on the vertex and those fringing the mandibles below. The clypeus in mature specimens almost invariably black, very rarely with two faintly traceable reddish maculations placed symmetrically one on each side. The labrum inclined to brownish or reddish. The mandibles chestnut brown to reddish over most of their surface, with as a rule only the teeth and the basal prominences black. The antennal sockets ferruginous. The scape usually

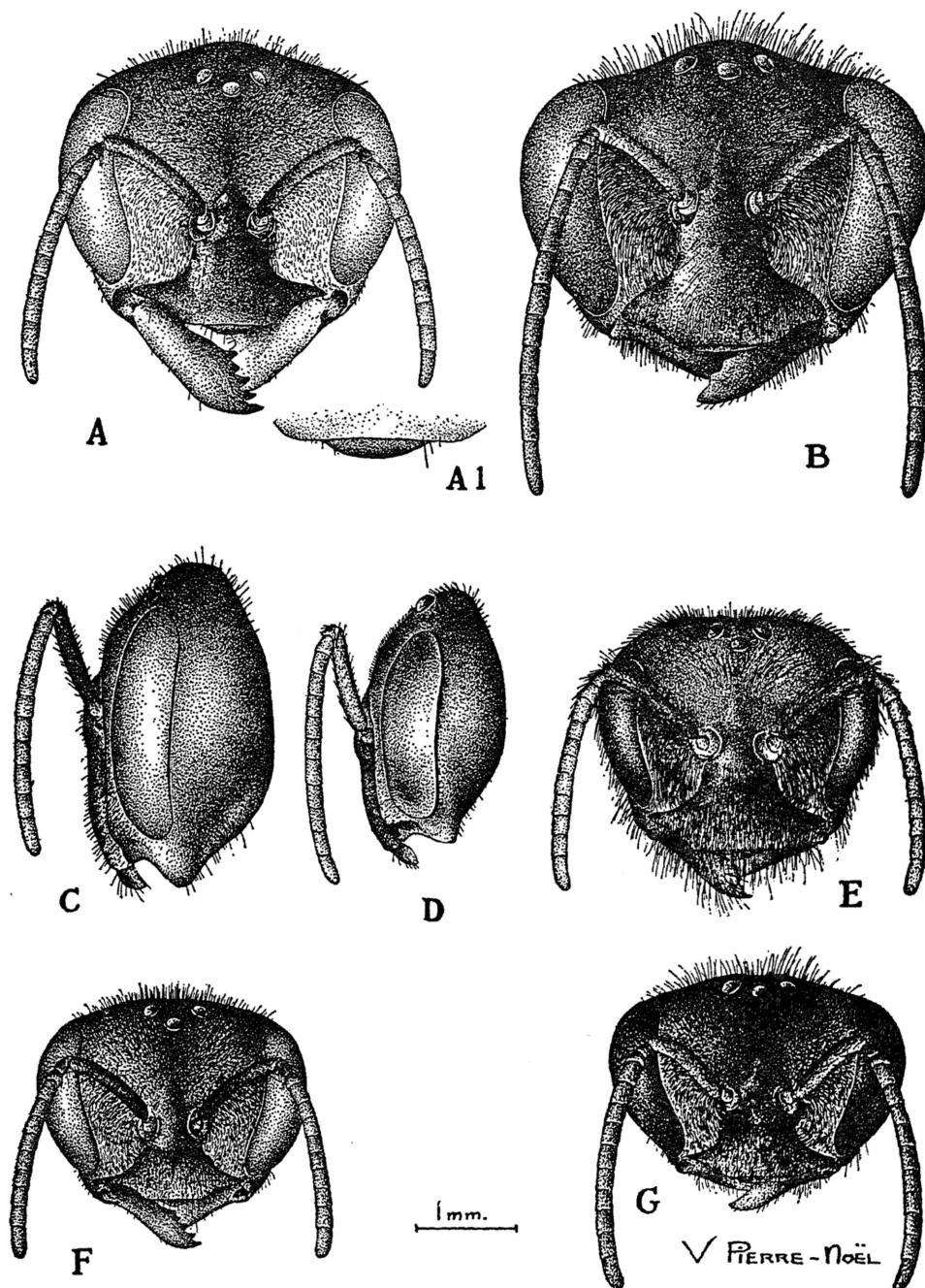


FIG. 21. A, A1. Head and labrum, respectively, of worker of *Trigona* (*Trigona*) *trinidadensis* variety *trinidadensis* (Provancher). B. Head of male. C. Head of worker of typical *trinidadensis* in profile, compared with (D) head in profile of worker of *Trigona* (*Trigona*) *trinidadensis* variety *silvestriana* Vachal; note the difference not only in size but in the character of the hairs on the front. E, F, G. Head of the queen, worker, and male, respectively, of *Trigona* (*Trigona*) *nigerrima* Cresson. Drawings by V. Pierre-Noël.

black with a more or less distinct to indistinct longitudinal brown stripe in front; the flagellum dark above, usually more or less brownish to reddish below, but sometimes almost uniformly dark both below and above.

THORAX: Black, of rather subdued sheen due to the presence of grayish tomentum on mesonotum, scutellum, pleura, and especially sides of propodeum in addition to the longer, more conspicuous, but sparser simple black hairs in these areas. The relative length of the hairs as indicated in the description of the subgenus *Trigona*.

LEGS: For the most part black or blackish, the fore and middle legs usually wholly so except for the frequently brownish to ferruginous tarsal joints (especially the apical one), but occasionally very largely reddish brown. The hind legs more variable, in many specimens dull brownish or reddish on at least the tibiae and tarsal joints; in others black, or black with a reddish area on the tibiae. The hind tibiae wide, clavate in outline, much wider at the apex than at the base; their anterior lateral contour gently emarginate; their posterior lateral contour strongly convex; their apex with an inconspicuous angle anteriorly that bears the comb; beyond this angle the apical contour has a curvilinear bulge, to be succeeded by an emargination, with the result that a rather strong, somewhat inwardly placed angle is formed where this apical emargination encounters the posterior contour of the joint; the outer face of the hind tibiae very gently arched over approximately its basal two-thirds, depressed to slightly excavated on approximately its apical one-third. The flattened area constituting the posterior part of the under side of the hind tibiae more than one-third the width of the joint towards the apex. The hind metatarsi about three-fifths as wide at their widest (near the apex) as the hind tibiae are wide at their widest, their posterior apical angle slightly acute. The hairs of the legs predominantly black but with the following relatively minor exceptions: the plumose hairs on the external face of the middle tibiae and extending usually to the basal part of the corresponding metatarsi dark brownish to blackish; the microscopic but stubby hairs on the elevated part of the under side of the hind tibiae and adjacent apical part beneath of the

hind femora silvery gray; suboval sericeous patch at the base of the under side of the hind metatarsi also silvery gray, although often the surface is covered with sticky matter concealing the true coloration; the metatarsal brushes blackish to more often copper colored or even golden depending a little on the angle from which the brushes are viewed. The relative length of the hairs and their distribution as indicated in the description of the worker of the subgenus *Trigona*.

WINGS: Very dark and conspicuously long. When the forewing overlays the hind wing, the brown color is so intensified that the median cell and the adjacent region of the wing appear to be approximately black, although actually they are of a nearly iodine stain. The apex of the wing of a somewhat lighter brown but without sharp transition. The transverse cubital veins feebly to sometimes rather strongly indicated. First discoidal cell about three-fourths as long as the marginal. Number of hamuli on each lower wing usually six, more rarely seven, very rarely as many as eight or as few as five. Of 330 wings examined, 251 had six hamuli, 59 had seven hamuli, 13 had five hamuli, and seven had eight hamuli, an average of 6.18. The tegulae of deep iodine stain to black.

ABDOMEN: Black or blackish, often more or less telescoped but in other cases not so, trigonate, approximating the thorax in width. Tergite 2 sometimes with a very few blotchy, shallow, scattered punctures over its shiny surface, and rarely such punctures occur also on tergite 1; on the subsequent tergites the integument has sometimes a granular appearance at the points where the hairs emerge but is otherwise smooth. The hairs black; minute, few, and appressed or semi-erect along the apex and sides of tergite 2, erect and moderately long on tergites 3 to 6 (but shorter usually than are the hairs on the corresponding tergites of *silvestriana*). Approximately the apical half of the sternites with erect black hairs at the middle and shorter hairs on each side; the tomentum on sternite 6 sometimes yellowish to brownish rather than black and the erect hairs on this sternite relatively few. When the abdomen is telescoped, the hair bands form a continuously hairy surface.

MEASUREMENTS: Specimens with compressed abdomen sometimes only 6 mm. in length, but usually the worker is from 7.5 to 11 mm. long; thorax width 2.75 to about 4 mm.; length of forewing, including tegula, 9.5 to 11 mm.

QUEEN (GRAVID)¹

HEAD: Barely wider than the mesonotum, not nearly so wide as the distance between the outer rim of one of the tegulae and the outer rim of the other. The facial quad-angle wide, the distance between the compound eyes at the level just below the middle ocellus about equal to the distance separating the middle ocellus from the apical margin of the clypeus. The eyes almost parallel to each other, scarcely convergent below, shorter than those of the worker from the same nest (a little more than two-thirds as long) and very notably narrower. In the specimen on which this description is based the eyes are very finely and sparsely hairy. The clypeus gently arched but, unlike that of the worker, not foveate at the apex medianly. The width of the clypeus, measured from one apicolateral extremity to the other, somewhat more than twice its length. The supraclypeus, like the clypeus, raised somewhat above the sides of the face. The labrum simple, triangular to rounded in apical contour and somewhat tuberculate at the middle of the apex. The mandibles distinctly toothed from end to end of the apex (five teeth in all). The malar space emphatically long, the distance between the lower extremity of the eye and the base of the mandible being somewhat under one-fourth the length of the eye and about twice the width of the flagellum. The ocelli small and remote from the compound eyes, the distance separating the lateral ocelli from each other being barely more than half that between each lateral ocellus and the nearest compound eye. The carina behind the ocelli low and much less conspicuous than in the worker, barely qualifying as a carina. More or less moderately shiny are all parts of the head to the inclusion of the sides of the face and the genal area, which, unlike that of the worker, is not pruinose. In the character of her hairs,

the queen of *trinidadiansis* contrasts sharply with the queens of *amalthaea* and *pallida*, the hairs (particularly those on the lower half of the head) being rather long, irregular, and shaggy instead of short and sericeous. The fulvous hairs fringing the lower edge of the mandible are as long as, or longer than, the mandible is wide at the base and notably longer than the hairs on the vertex, which are likewise fulvous. The mandible has hairs not only along its lower margin but also over its outer face. The more or less fulvous to grayish hairs on the labrum and clypeus also relatively long. The hairs of the front are relatively short as are those of the genal area, being grayish in both areas, and in the case of those of the front not or scarcely increasing in size upward. The rather soft hairs of the scape abundant and conspicuous but shorter than the scape. The chitin predominantly black. The labrum and mandibles, unlike those of the worker, black except that in the case of the mandibles there is a brownish area occupying about the apical one-third of the mandible but not to the inclusion of the black teeth. The antennal sockets and under side of the flagellum ferruginous to light brownish in contrast to the darker upper side of the flagellum and the black scape, which is distinctly wider than the flagellum and about one-half as long.

THORAX: Black, to here and there brownish (particularly on the pleura and propodeum), wider than that of the worker from the same nest. The length of the mesonotum plus scutellum a little greater than the width of the mesonotum at the base. Contrary to the condition in the worker there is little or no tomentum and hence somewhat greater shininess. The hairs are ochraceous to reddish fuscous and tend to be lighter on the lower part of the mesopleura than on the upper half; the hairs on the mesonotum are relatively short and for the most part only semi-erect, but those on the mesopleura and particularly those on the scutellum are notably long. The middle area of propodeum hairless and shiny.

LEGS: Reddish brown to in part black, with the femora rather more uniformly dark than the tibiae, and the hind tibiae red on the anterior one-half of their external face and contrastingly black on the posterior half of

¹ Description based on a single specimen from San Ramon, Valle de Chanchamayo, Peru.

that face (very possibly not a constant character). The small joints of the tarsi (particularly the apical joint) reddish. The hind tibiae barely longer than the combined length of the hind trochanters and femora, somewhat clavate in outline, their apex feebly rounded anteriorly and with a feeble corner posteriorly. The hind metatarsi approximately three-fifths the width of the apex of the hind tibiae and slightly tapering from near the base to the apex; the combined small joints of the hind tarsi about five-sixths as long as the metatarsi when measured along the inner face; the inner face of the hind metatarsi uniformly covered with soft, yellow golden hairs of rather even length. The under side of the fore and middle metatarsi with hairs of approximately the same color. The other hairs of the legs more yellowish gray and a little coarse, the hairs being predominantly simple. The hairs are fairly long on the under side of the middle and hind trochanters and on the hind coxae. The femora are moderately hairy on their outer (anterior) and under side but relatively glabrous on their inner (posterior) face. The hairs on the outer face of all the tibiae (including the third pair) are relatively dense, the contrast in length between the hairs of the outer face of the middle tibiae and those of the outer face of the fore tibiae far less than in the corresponding areas of the worker. The outer face of the middle tibiae virtually lacks the plumose hairs that in the conspecific worker are abundantly intermixed with the simple hairs of this joint; the plumose hairs in the poorly defined posterior lateral fringe of the hind tibiae short, undeveloped, and difficult to distinguish from the simple hairs. The hairs of the posterior fringe of the metatarsi longer than the hairs on the outer face of these joints or anteriorly.

WINGS: Smoky, shorter than in the worker, probably failing to reach the apex of the third tergite of the abdomen, but their precise length difficult to determine accurately owing to their mutilated condition. Tegulae rufo-fuscous. Number of hamuli in one hind wing six.

ABDOMEN: Dark brownish to blackish. Tergite 1 smooth and hairless except for moderately long if somewhat sparse hairs laterally at the apex. The subsequent ter-

gites covered rather densely with, on the whole, a woolly growth of hairs of grayish to fulvous hue, the basal parts of the tergites in the specimen before me being exposed, as are the apical parts, and even more densely (concealingly) hairy. The hairs shorter on tergite 6 than on the tergites preceding. Punctuation on the apical one-half of tergites 2 to 6. Erect, rather fulvous hairs along the apical one-half of sternites 2 to 5.

MEASUREMENTS: Length about 10 mm. (of which the abdomen accounts for considerably more than one-half); width of thorax somewhat under 4 mm.; length of forewing uncertain owing to mutilation.

MALE¹

HEAD (FIG. 21B): Black. The facial quadrangle not so wide relatively as that of the worker. The distance from one eye to the other at their level of closest approximation (below) only about four-fifths of the length of the eye, whereas in the worker the distance separating one eye from the other at the corresponding level is about equal to the length of the eye. The clypeus and supraclypeus raised a little above the sides of the face, the clypeus very gently arched, barely foveate at the middle of the apex, its apicolateral angles acute and relatively remote from the eye, the intervening distance approximating the width of the basal joints of the flagellum; the length of the clypeus about three-fifths its greatest width. The labrum simple. The mandibles obtusely tridentate along the receding apical edge. Feeble as is the dentition of the mandibles, it is nevertheless much more distinct than in the males of the other species of subgenus *Trigona* from which the males are known. In contrast to the largely reddish or brownish mandible of the worker, the mandible of the male is black with a narrow red stripe just basad of the apex. The malar space relatively well defined, about as long at its middle as the joints towards the base of the apically tapering flagellum are wide. The distance between the lateral ocelli barely greater than that which separates each from the nearest compound eye. The whole face duller and more

¹ Description based on two specimens: one from La Chorrera, and the other collected between La Chorrera and La Sombra, Peru.

hirsute than that of the worker. The clypeus with many more and longer black hairs (in addition to the silvery gray appressed hairs) than are present on the clypeus of the worker, with the result that the integument appears more or less coarsely dotted (where the bristles emerge) instead of smooth. Even on the sides of the face erect black hairs are rather plentiful in addition to the appressed, almost scale-like, silvery gray tomentum. Black

THORAX: Black, a little more shiny than the head, although lightly covered with grayish to dark tomentum (the tomentum more distinctly gray and dense on each side of the propodeum). The erect hairs of the thorax and propodeum black.

LEGS: Brownish (particularly the hind pair) to blackish. The hind tibiae feebly concave along their anterior lateral contour and much more emphatically convex along

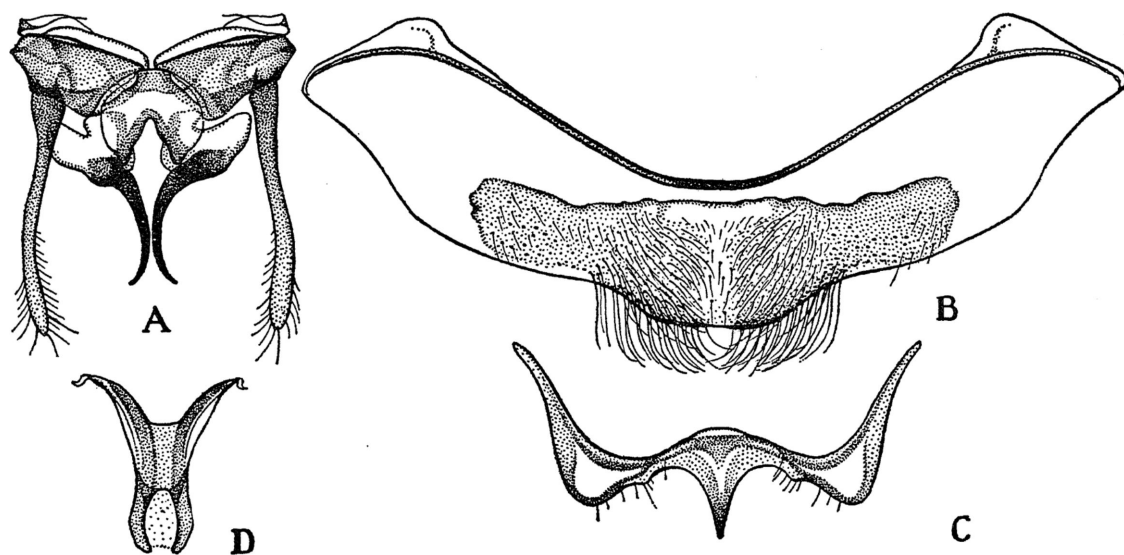


FIG. 22. Abdominal parts of male of *Trigona* (*Trigona*) *trinidadensis* variety *trinidadensis* (Provancher). A. Genitalia (chitinized parts only). B. Sternite 5. C. Sternite 6. D. Sternite 7. All based on a specimen from La Chorrera, Peru. Drawings by Shirley H. Risser.

hairs occur also on the front and on the scape (those on the scape almost as long as the scape is wide but definitely shorter than those on the lower half of the clypeus). The black hairs on the vertex are long and coarse as are those on the labrum and those fringing the inferior margin of the mandibles. The mandibular hairs are black like the erect hairs on the other parts of the head, not more or less copper colored as are those in the corresponding area of the worker. Interspersed among the dense scale-like tomentum of the upper two-thirds of the genal area are some short inconspicuous black hairs, while the tomentumless lower one-third has longish black hairs. The antennal sockets ferruginous; the black scape with a ferruginous stripe in front; the flagellum black above, more or less ferruginous below.

their posterior lateral contour; the contour of their apex somewhat irregularly rounded anteriorly and subangulate posteriorly; their outer face much flattened posteriorly towards the apex, even a little concave; their greatest width (near the apex) about four-fifths that of the conspecific worker from the same locality at the corresponding level. The hind metatarsi towards the apex about three-fifths as wide as the hind tibiae; like the associated tibiae the hind metatarsi are a little thickened anteriorly, flattened posteriorly; their posterior apical extremity is slightly acute to rounded. The hairs of the legs predominantly black or blackish, with the following relatively minor exceptions: the tomentum of the under side of the trochanters (more especially the first pair) somewhat dull grayish; the short bristles at the

apex of the inner face of the hind femora and the similar dense short bristles down the elevated area of the under side of the hind tibiae, as well as the sericeous flattened hairs at the base of the under side of the hind metatarsi silvery gray; the more erect hairs on the apical two-thirds of the under side of the hind metatarsi more or less copper colored. The fringe along the posterior lateral contour of the hind tibiae mainly plumose, the longer simple hairs of this fringe fully one-half as long as the tibiae are wide. The distribution of the simple black hairs in general and their relative length approximately as indicated in the generalized description of the male of subgenus *Trigona*.

WINGS: As in the worker, dark and conspicuously long. Of the four wings available for examination, three had six hamuli and one had five hamuli, an average of 5.75.

ABDOMEN: Black or blackish, comparable in width with the thorax. The hairs of the tergites black; those of tergite 2 appressed, forming a narrow band along the apex; those of tergite 3 semi-erect and forming a broader band along the apex; those of the subsequent tergites longer (much longer than the hairs on the sternites) and more erect; tergite 7 with a fringe of black incurved hairs that give a rather strongly hirsute appearance to the apex. The sternites with more or less erect black hairs towards the middle of their respective apices and sericeous hairs on each side of them. For the structure of the sternites and the genitalia, see figure 22.

MEASUREMENTS: Length 8.5 to 11 mm. (abdomen extended in the specimen of maximum length); width of thorax 3.5 to 3.75 mm.; length of forewing, including tegula, 10.5 to 10.75 mm.

TYPE MATERIAL

In the Provancher collection in the Public Museum at Quebec is a specimen of *trinidensis* numbered 1537. The name label has a double red line around the margin, which indicates that the insect belongs to what has been designated the *dernière* Provancher collection, because, in contradistinction to a collection acquired by the museum during Provancher's lifetime, the *dernière* collection was retained and used by Provancher up to the time of his death, passing into the pos-

session of the museum subsequently through purchase. It was from specimens assignable to the *dernière* Provancher collection that Gahan and Rohwer established lectotypes for the Provancher species of Hymenoptera other than Apoidea unless there was something in the description or manuscript notes to prevent. Similarly No. 1537 may be designated the lectotype of *trinidensis*. There is a second specimen of *trinidensis* in the Provancher collection which lacks a number. As the name implies, *trinidensis* was described from the Island of Trinidad.

DISCUSSION

This is the insect that a number of writers have interpreted as *amalihea* (see discussion under *amalihea*) but that others, in disagreement with that interpretation, have been referring to as *silvestriana*. Friese (1909a, p. 39; 1917, p. 299), one of the adherents of the viewpoint that the insect is *amalihea*, made Provancher's *trinidensis* a synonym of *amalihea*. Cockerell (1925c, pp. 626-627) likewise voiced the suspicion that an earlier name might be Provancher's *trinidensis*. I have had a chance to examine Provancher's type material in the Public Museum in Quebec and find that *trinidensis* and Vachal's South American specimens of *silvestriana* are the same insect. As *trinidensis* has priority, it must henceforth supersede *silvestriana* as the name for the species and typical variety. The name *trinidensis* variety *silvestriana* will, on the other hand, apply to those specimens in the original type material of Vachal which he reported from British Honduras. Undoubtedly, I think, these must accord with all of the other Central American specimens of *trinidensis* that I have had opportunity of examining in presenting well-defined differences from the South American variety.

The typical variety of *trinidensis*, as might be inferred from its wide range in South America, is not wholly stabilized in its characters, and little differences are discoverable between representatives of one locality and those of another, but it is doubtful whether these differences are of sufficient importance to justify varietal names. Cockerell (1925c, pp. 626-627) has separated, as a variety *rohweri*, specimens taken by Hester

M. Rohwer in Trinidad, citing among the differences smaller size (9 mm. as against 11 mm. specified by Vachal) and "dark fuliginous instead of reddish wings." As a general rule the *trinidensis* of a particular locality are fairly uniform in size, but this does not apply to larger geographic areas, or even wholly within a locality. Some of the largest individuals in the collection before me are from San Ramon in the Valle de Chanchamayo, Peru, and from La Chorrera to La Sombra in the Putumayo District of Peru; some of the smallest are from El Campamento, likewise in Peru; but among the specimens from El Campamento are some that are comparable in size with the large individuals from the other Peruvian localities mentioned. Iquitos, Peru, also offers individuals of contrasted size, a specimen taken in March being distinctly larger than a series from the same locality collected in June. Similarly among the Bolivian specimens those from Rurrenabaque are for the most part smaller than those from Huachi, Río Beni, while the latter in turn yield in size to those from Ivon, Río Beni, and San Georgio. Comparable diversity of size occurs among the Colombian and also among the Brazilian specimens. However, the specimens from South America average larger than those of the variety *silvestriana* from Central America and have on the whole greater wing length. Certainly there are no individuals in the collections from Central America that are comparable in size either to the larger Peruvian, Bolivian, and British Guianan specimens or to the specimens in the present collection from localities in São Paulo and Minas Gerais.¹

The coloration of the wings is more uniform than is the size of the insect, although when the wings are spread the dark areas are less intensified than when the forewing overlies the hind wing. Most of the wings I should describe as "dark fuliginous" rather than as "red." Of all the specimens before me only those from Baurú, State of São Paulo, seem to have wings of a trifle more reddish stain; even in the case of these the effect is a light chocolate color barely differ-

entiated from the slightly darker wings of the other specimens.

Another direction of variability is in the structure of the clypeus. Usually the clypeus is of rather uniform surface basally, although foveate at the middle of the apex, but some specimens (more particularly the Peruvian ones from El Campamento, Hacienda San Juan, El Encanto, Huacapistana, and Huacapistana to San Ramon) have a faint line impressed from base to apex that, while not so groove-like as is the median, longitudinal depression in the clypeus of *ruficrus* or even *corvina*, is nevertheless easily traceable as a rule.

Faint bilateral markings of reddish tinge may now and then be detected on the clypeus of certain specimens, especially those from Trinidad, but probably these are merely vestiges of the callow state. The hind tibiae are variable in color, sometimes brown, sometimes black, sometimes with a patch of red on the middle of their outer face, as indicated by Cockerell for *rohweri*.

Other distinctions are probably merely the result of relatively large or relatively small size. Thus in large individuals, irrespective of locality, the malar space is apt to be more distinct than is the case in less robust individuals. In such individuals, too, the shallow, scattered punctation on the second abdominal tergite is apt to be more distinct than in the smaller individuals, in some of which it is all but absent. Vachal (1908, pp. 221-222) indicated that a difference between Olivier's *amalthaea* and his own *silvestriana* (the South American specimens in Vachal's type material are here considered the equivalent of Provancher's *trinidensis*) was the presence in *amalthaea* on the under side of the hind metatarsi of an area covered by silky hairs of silvery hue and the absence of such an area in *silvestriana*. But as Ducke (1910a, p. 108) has pointed out, this distinction does not hold generally, and one is inclined to believe that Vachal must have misinterpreted his specimens, so invariable, according to my studies, is the presence of this differentiated area on the metatarsi in all workers of the subgenus *Trigona*.

The male, hitherto unreported, is seemingly a rare creature. Of about 600 specimens, representing many different localities,

¹ Friese (1917, p. 299) awarded preëminence for size to specimens from Blumenau, which is in the State of Santa Catharina.

that are before me there are only three that can be assigned to this sex. One of these individuals (the male from Chapada) has smeared lightly over the broad surface of both of its hind tibiae some sticky substance, insufficient in quantity, however, to suggest an actual load. The other two males also have traces of sticky matter on the broad outer side of their tibiae, but less markedly so (see discussion of *Trigona*, p. 203). Provancher collected a large number of *trinidadiansis* but found no males among them (1888, p. 345), and H. von Ihering recorded (1912, p. 44) the absence of males in a nest from Franca, Brazil.

The reader will find an account of the various nest sites selected by *trinidadiansis* in the discussion of *amalthaea*, and in consequence the emphasis in the following paragraphs is more particularly on the architecture of the nest and the materials used. Provancher (1888, p. 345) stated that the external envelope of the nest appeared to be made of black earth pasted together with a liquid which hardened it in drying. This is more or less, too, the impression of Myers (1935b, pp. 131-134), who like Provancher reported a nest from Trinidad. "The outside," wrote Myers, "was covered with exceedingly hard, small-chambered resinous material, incorporated with much earth." There is no mention in either Provancher's account or that of Myers that leaves are employed as building material.

On the other hand, nests reported from Peru have macerated leaves in abundance in the outer envelope, and one is tempted to wonder whether there is a regional difference in building methods as illustrated by the examples (all too limited for a well-based conclusion) from these two areas. Let us proceed to a more detailed consideration of the architecture of these Peruvian nests.

An account and diagram of a nest of *trinidadiansis*¹ from Satipo, Peru, were published by Weyrauch (1942, pp. 62-64, fig. 6). The nest was externally placed, being supported by the forking branches of a tree, and consisted of four horizontally arranged combs that were connected with one another

by numerous minute pillars. Beneath the combs were many honey pots and pollen pots. Surrounding these brood combs and provision pots were a relatively narrow envelope of wax and beyond it towards the exterior a much larger enveloping wall consisting of six successive layers of a paste of macerated leaves. This involucre had many tiny pillars lending support to the structure and also numerous vacant spaces "for the purpose of maintaining in the interior of the nest a temperature higher than that of the surrounding atmosphere through the confinement of the air."

Like the above nest a second nest (pl. 5, fig. 1) which was noted by Weyrauch at San Ramon, Peru, on February 5, 1940, had an "outer envelope consisting of a thick mass of coarsely chewed leaves," in which orange leaves predominated. "This envelope," Dr. Weyrauch wrote me, "is thoroughly compact and contains no hollow spaces. Inward there follows a second envelope, which is wider than the first and consists of many relatively large hollow spaces, which form interconnecting galleries and are always occupied by a number of bees. These hollow spaces according to my measurements were 2 cm. by 2 cm., or 1.6 cm. by 3 cm. This second envelope that is made up of galleries is fashioned of a black substance consisting of finely chewed leaves intermixed with an abundance of black and very sticky resin. The galleries have a fine smooth surface within in contrast to the rough uneven surface of the outer envelope."

Proceeding inward there were next encountered the brown to black pots filled with pollen and then similarly shaped pots containing honey. The sizes of these pots were, according to Weyrauch's measurements, 1.4 cm. by 1.7 cm., 1.2 cm. by 1.5 cm., 1.3 cm. by 1.5 cm. They were always somewhat larger than the brood cells.

The brood cells were arranged in combs, 10 in all. The ordinary cells measured 5.2 mm. in width and 8 mm. in length; the royal cells, 1.1 cm. in width and 1.4 cm. in length. Weyrauch noted the position of two royal cells as being "in the middle of two different combs." This is at variance with the usual location of royal cells, which in most instances are recorded as being on the periphery of

¹ The nest was designated *Trigona* sp. in Weyrauch's published report, but I have since seen a specimen from the nest and it is *trinidadiansis*.

the combs. Weyrauch went on to say, "At the rim of some combs were individual honey pots which were somewhat larger than the brood cells but not so large as the rest of the provision containers." The area occupied by the combs was 10 cm. in width, 14 cm. in height, and 18 cm. in depth. The extent of the entire nest was 66 cm. in length, 56 cm. in width.

This nest was in a stone wall at a height of 1 meter. Externally it resembled "a large deposit of cow dung glued to the wall," and the exposed part projected beyond the wall for a distance of 14 cm. The nest entrance was funnel shaped, short, 6 cm., and 9 cm. in width at the orifice.

Yet another nest of this species observed by Weyrauch at San Ramon, on March 1, 1940, was attached to a cliff wall in a moist forest, at a height this time, of not 1 but 13 meters. The entrance tube was "cylindrical, of dark brown resin, 4 cm. wide, 12 cm. long." Apparently Weyrauch was unable to examine the interior of this nest, but it is interesting to note that, in the case of the other nests he examined, macerated leaves formed so important a building material in the construction of the envelope or envelopes of the nest. Yet another nest viewed by Weyrauch (at Santa Ana, Rio Urubamba) was located at the foot of a boulder.

The Peruvian nests have been noted in some detail because in certain respects they seem to differ, not only in the building materials used but even with respect to the architecture, from the nest described by Myers (1935b, pp. 131-134) from Trinidad. Let us cite for purposes of comparison the pertinent passage from Myers: "Within this [the outer envelope] were the combs, arranged horizontally one above the other, connected by quite thin pillars of resinous wax (cerumen). They formed areas of wide waxy-resinous labyrinths with large (half- to three-quarters of an inch in diameter), soft, thin-walled honey pots—stuck about in them at irregular intervals. The walls of these large passages showed also occasional small waxy patches of a pale colour, looking exactly like *Lecaniine* Coccids, for which I at first mistook them.

"The interior of the nest contained also localized areas of pollen stores, varying from

reddish to pale yellow in colour. Originally the pollen had been stored in large, more or less spherical cells, but these had apparently been packed so tightly and the whole so compacted that there were now only large botryoidal masses of hard caked pollen separated by thin skins of dark wax."

This nest was 38 inches long with a greatest diameter of about $2\frac{1}{2}$ feet. It had an entrance spout "about a foot long, with an opening two inches in diameter." In contrast Silvestri noted (1902b, p. 144) an entrance tube at Coxipò, Brazil, that he recorded as "about ten millimeters long and six in width." But these measurements, so in contrast not only with the dimensions of the tube of the nest from Trinidad but also of the nests from Peru, should possibly read centimeters, not millimeters. If the entry is correct, it would indeed point to an emphatic difference in size.

It seems appropriate for purposes of comparison to include also a translation of H. von Ihering's account (1912, p. 44) of a nest of presumably this species from Franca, São Paulo, Brazil. The name used is *friesei*, which von Ihering had previously (1903, p. 204) applied to *amalthaea* in the sense of *fuscipennis* but, as Vachal determined von Ihering's specimens from this nest as his own *silvestriana*, there can be little doubt that the nest was fabricated by the species we are here considering.

"A nest of this species (No. 1949)," wrote von Ihering, "was sent to me in July 1903 by Mr. Dreher from Franca. It was located about six meters high in a hollow tree in a dense forest, and the entrance consisted of a simple round opening. The whole nest occupied about one meter of the extent of the hollow. Beside the brood mass there were present irregularly heaped-up provision pots in large number which on the outer side merged into a net work of irregular cables and beams. The latter presented a particular peculiarity of the species, in that seemingly they were fashioned of dung, apparently that of horses. . . .

"A further peculiarity was presented by the brood combs, which lacked communicating holes and were attached to one another by exceedingly thick waxen pillars four to six millimeters wide by eight millimeters

high. The cells were nine millimeters in length by 4.7 millimeters in diameter. There were two royal cells thirteen millimeters in length and of the usual oval form. . . The nearly spherical provision pots were relatively small, from eighteen to twenty-two millimeters in diameter and contained predominantly pollen, of which the color was in some of the pots yellowish white, in others dark red."

According to Provancher (1888, p. 344) *trinidadensis* visits the flowers of the banana, and indeed his first specimens were secured there.

Myers listed *trinidadensis* among the bees injurious to grapefruit and other *Citrus* (1935b, p. 134). According to his observations, *trinidadensis* gnaws bark from the trunk and main branches, and nips off wholly or partly the young green shoots as well as actually biting into the fruit. Myers added this further observation and conclusion:

"The same species was observed at Mt. St. Benedict, Trinidad . . . attacking large old trees (7-8 inches in diameter) of sour orange growing among cacao. They were cutting in the trunk hundreds of openings 1-2 cm. across and roughly circular. Two trees, widely separated, were thus affected. It is thus probably an old habit, not a new one originating since the recent introduction of grape-fruit culture."

Attacks on the bark of other trees by *trinidadensis* noted in the section of the Introduction on foraging and materials foraged (p. 107) confirms Myers' impression that the habit may be an old one.

A probable explanation of this nibbling, reminiscent of a similar destructiveness in *amalthea*, is that the bee is endeavoring to get at the sap or gum. In confirmation of this impression is the fact that Salt (1929, p. 444) observed bees of the species *trinidadensis* in Colombia engaged in "collecting gum from scars in the bark of Eucalyptus trees," and more recently Weyrauch wrote me that he had seen these bees similarly engaged on the trunk of a eucalyptus at Oxapampa, Peru, while at Satipo, Peru, they were sucking sap on a tree the name of which is not noted.

Myers' reference to the attack on green shoots of *Citrus* brings to mind the employment of macerated *Citrus* leaves in the con-

struction of the Peruvian nests and in turn makes for hesitancy in accepting the conclusion suggested very tentatively in a previous paragraph that there may be a more or less marked difference in the use of building materials of *trinidadensis* as between Peru and the island from which this bee was originally described.

Hermann von Ihering (1903, p. 204) noted the habit of *trinidadensis* to alight on carcasses as well as on cow dung and other excrement.

Provancher (1888, p. 345) noted that bees of this species attacked him with full ferocity when he attempted to mutilate their nest, and Myers (1935b, p. 131) also testified to their aggressiveness when molested. What these authors record for the Trinidad representatives of the species Silvestri confirmed also for individuals from Coxipò (1902b, p. 144) and H. von Ihering for individuals from southern Brazil, the terms used by the latter author being "very wild by nature" (1903, p. 204) and "exceedingly violent" (1912, p. 44).

The honey of *trinidadensis* was described by Myers (1935b, p. 132) as "very dark, fairly thin and very sweet. Litmus showed it to be extremely acid." These are terms very similar to those in which Fermin long previously (1769, p. 301) extolled the honey of the bee he called *sylvestris* (from Surinam), which may possibly have been *trinidadensis*: "It is always liquid, it is of the color of amber, and very sweet, but it turns sour easily and in short time."

Myers found a total of 24 species of inquilines in a single nest of *trinidadensis*, although one of these at least, the bee *Augochlora*, would seem probably to have been only a casual visitor (1935b, p. 134).

F. Monteverde observed *trinidadensis* swarming but gave no further details. The notation appears on the label attached to his specimens from El Valle, Venezuela.

The popular name of this bee in the Brazilian states of Matto Grosso and São Paulo is "sanharó" or "sanharão" (H. von Ihering, 1903, pp. 204, 277; 1904b, p. 381; Ducke, 1916, p. 134; 1925, p. 344; 1945, p. 101; R. von Ihering, 1940, pp. 705, 880). H. von Ihering stated (1903, p. 277; 1904b, p. 381) that this bee derives its name from its wild

and malicious nature, "sanharó" being a corruption of "nharó" or "nharon." In the Tupi (or more specifically Guarini) tongue "nharoncaba" means anger.

DISTRIBUTION

As here delimited, the typical variety is found abundantly in Colombia and Venezuela; there is a single record from British Guiana, but it has not yet been reported with certainty from Dutch or French Guiana. Along the west coast of South America it occurs in Ecuador, Peru, and Bolivia. In Brazil it extends from Amazonas and Acre Territorium in the north to as far south as the State of São Paulo and even Santa Catharina (Blumenau record of Friese). Ducke (1925, p. 422) included localities also from the States of Pará, Matto Grosso, Maranhão, and cited Vachal's record (1908, p. 222) from the State of Goyaz. But in some of these areas it is seemingly of spotty distribution. Ducke noted its absence from the greater part of the State of Pará, in the case of Matto Grosso reported it only from the northern and central part of the state, and in the case of Maranhão from the southern part only of that state. He indicated furthermore its absence from areas in Brazil, located near the Atlantic, comparing it in this respect to *limão*.

In Central America its place is taken by the variety *silvestriana* as represented by Vachal's type material from British Honduras. Somewhat surprisingly there are, however, three specimens before me of typical *trinidadensis* marked "Mexico, Peab. Acad." These specimens, if correctly labeled, would seem to be lone outposts of this form. In the collections under examination typical *trinidadensis* is represented from the following South American localities:

COLOMBIA: Caldas, 4400 feet, May 9-14, 1914 (H. S. Parish); La Cumbre, 6600 feet, May 19, 1914 (H. S. Parish); Cartagena, Jan. 1, 1921 (E. W. Deming); Cincinnati, Feb., 1924 (H. W. Atkinson); Vista Nieve, Santa Marta, 5000 feet, Feb. 10, 1927 (G. Salt); Cerro Patron, Río Frio, Magdalena, 4000 feet, Aug. 1, 1927 (G. Salt); between Queremal and Buenaventura, 3500 to 4000 feet, Feb. 3 and Feb. 17, 1935 (J. Aranibar, E. I. Huntington, S. Quintero, and H. F. Schwarz); Cali District, western Cordillera, 5500 feet, Feb.

4, 1935 (H. F. Schwarz); Muzo, Department Boyacá, 900 meters, 1936 (J. Bequaert); Villavicencio, Department Meta, 450 meters, 1936 (J. Bequaert); Restrepo, Department Meta, 500 meters, 1936 (J. Bequaert); San Vicente de Chucurí, Department Santander, 500 meters, 1936 (J. Bequaert).

BRITISH GUIANA: Kuyuwini River, Nov. 22, 1937 (W. G. Hassler).

VENEZUELA: Lagunita de Aroa, 2000 feet (M. A. Carriker); Río Mato, in Caura District, Oct., 1909 (M. A. Carriker); Cariaquito, Jan., 1911 (S. Brown); Mt. Duida region, Fish Creek, Feb., 1928 (G. H. H. Tate); Caracas Valley, "Los Ruises," May 21, 1926; Caracas, Dec. 23, 1930 (J. G. Myers); north of Caracas, 3400 feet, March 21, 1907 (G. B. Longstaff); Guanta, Jan. 7, 1931 (J. G. Myers), and Aug. 20 (Pomerat); Las Adjuntas, 957 meters, June 16, 1926; Puerta La Cruz, July 7 (Hase); San Juan de Los Morros, June 3, 1934 (H. Farenholtz); El Valle, Nov. 8, 1938, swarming (F. Monteverde); Barinas (P. J. Anduze); Caripito, 1942 (H. S. Fleming).

TRINIDAD: Port-of-Spain, Jan. 1905 (August Busck), July 10, 1927 (Cornell Univ. Exped.), Aug. 24, 1934 (H. F. Schwarz); Coparo, Feb. 11, 1910; Caura, Sept. 25, 1930 (A. Pickles); Trinidad (F. W. Urich), 1914 (E. B. Connell), Oct. 6, 1930 (J. G. Myers), July 20 (W. M. Wheeler); San Fernando, Feb. 2, 1912 (G. A. K. Marshall), Aug. 16, 1924 (J. F. W. Pearson); Blue Basin, Aug. 17, 1924 (J. F. W. Pearson); Arima, Aug. 17-19, 1924 (J. F. W. Pearson); Maracas Fall, Aug. 19, 1924 (J. F. W. Pearson); Fyzabad, Dec. 1, 1924 (S. A. Neave); Quare River Valley, 1931 (A. K. Totten); St. Augustine, Nov. 28, 1934, and Dec. 31, 1934 (N. A. Weber); foothills north of Tunapuna, March 16, 1935 (N. A. Weber); Cumato (W. S. Brooks).

ECUADOR: Baños (R. Haensch); Mera, Jan. 25, 1923 (F. X. Williams); Napo, Río Pano, April 8, 1923 (F. X. Williams); Tena, Feb. 14, 1923, male, Feb. 23, 1923, March 16, 1923 (F. X. Williams); Río Pastaza, March 19, 1939 (F. M. Brown); Jatun Yacu, Río Napo watershed, 700 meters (W. C. MacIntyre).

BOLIVIA: Tarata, 1900; Huachi, Río Beni, Aug.-Sept. (W. M. Mann); Rurrenabaque, Río Beni, Oct. (W. M. Mann); San Georgio, Río Beni, Oct. (W. M. Mann); Ivon, Río Beni, Feb. (W. M. Mann).

PERU: Río Charapa, Sept. 13, 1911 (C. H. Townsend); Yurimaguas, March 26, 1920 (H. Parish); Iquitos, June, 1920 (H. Parish), July 28, 1920 (Cornell Univ. Exped.); Río Napo, June-July, 1920 (H. Parish); Huacapistana, Río Tarma, June 1-2, 1920 (Cornell Univ. Exped.); Huacapistana to San Ramon, Río Tarma, June 3, 1920

(Cornell Univ. Exped.); Hacienda No. 2, Colony of the Perené, June 15, 1920 (Cornell Univ. Exped.); La Merced, Río Chanchamayo, June 17, 1920 (Cornell Univ. Exped.); El Campamento, Colony of the Perené, June 18-19, 1920 (Cornell Univ. Exped.); Hda. San Juan, Colony of the Perené, June 16 and 23, 1920 (Cornell Univ. Exped.); Tambo Eneñas, Cam. del Pichis, July 4, 1920 (Cornell Univ. Exped.); Dos de Mayo to El Porvenir, Cam. del Pichis, July 6, 1920 (Cornell Univ. Exped.); Puerto Bermudez, Río Pichis, July 12-19, 1920 (Cornell Univ. Exped.); Río Cotuhé, Aug. 12, 1920 (Cornell Univ. Exped.). Putumayo District: La Chorrera, Aug. 17-20, 1920 (Cornell Univ. Exped.); La Chorrera to La Sombra, Aug. 21, 1920, male as well as workers (Cornell Univ. Exped.); La Sombra, Aug. 22, 1920 (Cornell Univ. Exped.); El Encanto, Aug. 25-27, 1920 (Cornell Univ. Exped.). Middle Río Ucayali, Nov. 27, 1923 (H. Bassler); Río Tapiche, Dec. 14, 1923 (H. Bassler); Iquitos, June 5, 1924 (H. Bassler); Río Santiago, Sept. 9, 1924 (H. Bassler); upper Río Marañon, Sept. 25, 1924 (H. Bassler); northeastern Peru (H. Bassler); San Ramon, Feb. 5, 1940, No. 8, and March 1, 1940, No. 31 (W. Weyrauch); La Merced, March 2, 1940, on rotting banana (W. Weyrauch); Valle de Chanchamayo, 800 meters, Nos. 45, 164, and 175 (W. Weyrauch); Santa Ana, Río Urubamba, 1300 meters, 1940, No. 143 (W. Weyrauch); Satipo, 600 meters, Nos. 124, 166 (W. Weyrauch); Oxapampa, 800 meters, March 15, 1940, No. 57 (W. Weyrauch); Tingo Maria, Río Huallaga, 700 meters, April 1, 1940 (W. Weyrauch).

BRAZIL: State of Amazonas: Esperanza, Aug. 9, 1920 (Cornell Univ. Exped.); Pôrto Velho (Mann and Baker); Río Içá-Putumayo, Aug. 11, 1920 (Cornell Univ. Exped.). State of Matto Grosso: Matto Grosso (Spencer Moore); Chapada (probably Sant' Anna do Chapada), male as well as workers (H. H. Smith); Cicade Branco, Pôrto Velho, Aug. 20, 1943 (M. Taylor). State of São Paulo: São Paulo, 1903; Baurú; Jundiahy, 1898; Avandandava. State of Minas Gerais: Lassance, Nov. 9-19, 1929 (Cornell Univ. Exped.).

***Trigona (Trigona) trinidadensis* variety
silvestriana Vachal**

Trigona silvestriana VACHAL, 1908, pp. 221-222 (specimens from British Honduras).

Trigona nigerrima, COCKERELL, 1912c, p. 312 (specimens from Quirigua,¹ Guatemala).

Trigona nigerrima, COCKERELL, 1913a, p. 10.

¹ A specimen of *silvestriana* from Quirigua, with Cockerell's identification as *nigerrima*, has been lent me by Cornell University.

Trigona nigerrima, WHEELER, 1913, p. 2 (identified by T. D. A. Cockerell).

Trigona amalthea, FRIESE, 1917, pp. 288, 299 (in part).

Trigona nigerrima, LUTZ AND COCKERELL, 1920, p. 499.

Trigona amalthea variety *borealis* FRIESE (specimens from San Mateo, Costa Rica, thus labeled and bearing in addition a type label. This would seem to be a manuscript name, as I do not find it in the literature).

Trigona nigerrima, LUTZ, 1924a, pp. 210, 216.

Trigona silvestriana, M. BATES, 1933, p. 47.

Trigona trinidadensis subspecies *silvestriana*, SCHWARZ, 1934, pp. 4, 11.

WORKER

DIAGNOSTIC CHARACTERS (FIG. 21D): Head differs from that of typical *trinidadensis* in having on the front an exceedingly low, dense, even growth of erect microscopic black hairs that are so short that they are traceable only when the head is viewed from the side. Contrasted with the coarse hair on the vertex, these minute hairs on the front seem of a different character and quality,

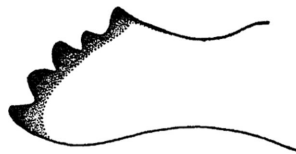


FIG. 23. Mandible of worker of *Trigona (Trigona) trinidadensis* variety *silvestriana* Vachal. Drawing by Elena Feld.

whereas in typical *trinidadensis* the hairs on the front are relatively coarse and uneven and grade into those on the vertex. The clypeus of *silvestriana* (unlike typical *trinidadensis*) has no erect black hairs, only microscopic silvery gray appressed hairs. The hairs of the scape are fine and very short, down-like, while those of *trinidadensis* tend to be coarse.

THORAX: As described for typical *trinidadensis*.

LEGS: See discussion, pages 257-258.

WINGS: Like those of typical *trinidadensis* but shorter. Number of hamuli per lower wing is usually six, more rarely seven, very exceptionally five. Of 81 wings examined 67 had six hamuli, 13 had seven hamuli, and one had five hamuli, an average of 6.15. The tegulae of deep iodine stain to black.

ABDOMEN: Like that of the typical variety but the hairs on tergites 2 to 6 usually longer, relatively if not actually, than the comparable hairs on the tergites, and especially tergite 3, of the typical variety.

MEASUREMENTS: Length 6.5 to 8.5 mm.; width of thorax 2.5 to 3 mm.; length of forewing, including tegula, about 9 to 9.5 mm.

QUEEN

Unknown.

MALE

Unknown.

TYPE MATERIAL

The types of Vachal's Hymenoptera were placed in the Muséum d'Histoire Naturelle in Paris, and it is probable that *silvestriana* was among them.

DISCUSSION

The material on which Vachal's designation of *silvestriana* is based was composite, including specimens not only from South America but also from British Honduras. The South American specimens are the same insect that Provancher had previously described as *trinidensis* and the name *silvestriana* can survive only as a variety applicable to the British Honduran specimens in Vachal's collection.¹ These presumably shared the characters that differentiate all the Central American examples of the species *trinidensis* that I have had occasion to examine.

In a rather striking way this variety of *trinidensis*, which is almost exclusively confined to Central America, shares some of the characters that differentiate *amalihea*, well represented throughout Central Amer-

ica, from its near relative in South America, *recurva*. The restricted development of the hairs of the face and their absence from certain areas characterize both *trinidensis* variety *silvestriana* and *amalihea*. But while other supplementary structural characters make for a specific separation between *amalihea* and *recurva*, typical *trinidensis* and *trinidensis* variety *silvestriana* are in

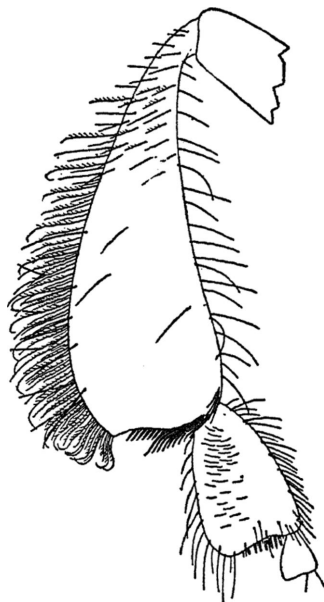


FIG. 24. Hind tibia and metatarsus of worker of *Trigona (Trigona) trinidensis* variety *silvestriana* Vachal. Drawing by Elena Feld.

most respects too closely allied to be sundered as distinct species even though geographically they are rather sharply divided. The variety *silvestriana* has been frequently confused with *nigerrima* (see discussion of that species, p. 286).

Judging from the specimens available, the presence of an incised longitudinal line on the clypeus is of far rarer occurrence in this variety than in typical *trinidensis*. Only in one or two specimens is this faint line traceable, and even in such cases it is confined to the basal half of the clypeus.

Among the specimens here referred to *silvestriana* the hind tibiae (fig. 24) and hind metatarsi are in the great majority of cases ferruginous to reddish, so that one is tempted

¹ In his paper of 1912 H. von Ihering took the position (p. 44) that the name *silvestrii*, established in 1902 for a *Trigona* distinct from *silvestriana*, should preclude the use of the latter name, which Vachal bestowed in 1908 upon the insect here discussed. However, other writers have continued to use the names *silvestrii* and *silvestriana* without resulting confusion and they would seem to have authority for so doing. According to the Entomological Code (1912) such endings as "i" and "ana" would not necessarily make the names homonyms, and in the Code of Nomenclature adopted by the Ornithologists Union (1908), such endings are considered distinct and not homonyms. Therefore, *silvestriana* is here retained.

to believe that the contrast between the hind legs on the one hand and the fore and middle legs on the other is more constant and emphatic than in typical *trinidensis*. On the other hand, many of the specimens characterized by the lighter coloration of the joints of the hind leg likewise have a ferruginous area apically on the clypeus, and it is likely that the lighter coloration on clypeus and hind leg is not so characteristic of the form *silvestriana* as it is of the degree of maturity of the individuals thus colored, which are probably callows.

Mr. Ferdinand Nevermann has written me regarding the partiality of *silvestriana* for building nests in the open in contradistinction to those built in tree hollows: "During the 28 years here in Costa Rica, I destroyed at least 10 to 15 nests of *silvestriana*, as this bee is doing most of the damage to the bananas and fruit trees, and all these nests were open nests just like the *Nasutitermes* nests, often hidden partly under tree-bromeliads. Since I started to study the nests, I found two under bromeliads and orchids, one on a large liana and one built flat on to the trunk of a palm (*Acantorrhiza albida*), where the long spines were supporting it."

Mr. Nevermann then went on to explain that in the last-mentioned instance the nest was begun in a foundation of interwoven spines just as in other cases the start was made in the roots of epiphytes. The nests, he stated, are "very large, up to 80 cm. high, and the funnel of the entrance is conspicuous."

Among the flowers visited by what Cockerell interpreted as *nigerrima* (1912c, p. 312) but which more likely was *silvestriana* were *Pontederia cordata*, *Ipomoea sidaefolia*, and *Centrosema plumieri*; Wheeler reported *silvestriana* (1913, p. 2) on flowers in the banana plantations; W. M. Mann observed it on sweet potato.

The ravages of *silvestriana* among *Citrus* groves in Honduras are set forth by M. Bates (1933, p. 47), who links *silvestriana* with *amalihea* as the worst pest of *Citrus* fruits (see *amalihea*, p. 220). Ballou (1945, p. 129) referred to it as opening holes in the bark of *Mammea americana* Linnaeus and as scarring the fruit of the banana, *Musa paradisiaca* Linnaeus.

DISTRIBUTION

Trigona trinidensis variety *silvestriana* occurs throughout Central America (with the possible exception of El Salvador) but is replaced in South America by the typical form. Only from Ecuador¹ have I seen specimens that can be referred to the form *silvestriana*, although typical *trinidensis* also occurs in that state. It is likely, however, that *silvestriana* is to be found also in Colombia, for Friese (1917, p. 299) stated with regard to *amalihea* (which, as conceived by Friese, is identical with *trinidensis*) that it is variable in size and sculpture as well as in color and that "the largest form lives in Blumenau, the smallest in the highlands of Colombia and Ecuador." It may well be, therefore, that what has here been delimited as *silvestriana* occurs in places in Colombia as well as Ecuador, although specimens from Colombia that I have examined (many of them from the highlands) have all been typical *trinidensis*, while Ecuadoran specimens of *silvestriana* came from relatively low altitudes as the above records indicate. Ballou (1945, p. 129) even recorded it from Venezuela. Almost certainly, I think, the specimens from British Honduras that Vachal lumped with the South American variety would reveal the characteristics that have been emphasized in the present description. Cockerell (1912c, p. 312) raised the question whether Vachal's specimens from British Honduras were not Cresson's *nigerrima* but among the material before me from British Honduras are specimens of *silvestriana* as here delimited, which differs structurally from *nigerrima*. Moreover, the differences between *nigerrima* and *silvestriana* are such that Vachal would hardly have associated the former with the South American specimens of *trinidensis*, while the inclusion of the northern race, *silvestriana*, with the southern representatives of *trinidensis* would be far more understandable.

The following localities are represented in the collections here considered:

¹ This country alone, of all the South American countries, also harbors *Melipona favosa* variety *phenax* and *Trigona* (*Trigona*) *pallida* variety *ferricauda*, which, with this exception, appear to be restricted to Panama and the Canal Zone.

MEXICO: Cameron collection in British Museum, without specific locality.

BRITISH HONDURAS: Belize (Johnson); Río Hondo (Blancaneau); Benque Viejo (Father Stanton).

GUATEMALA: Department of Vera Paz: Pancina (Champion); San Juan (Champion); Tamahú (Champion); Cubilguitz (Champion); Cacao, Trece Aguas (Barber and Schwarz), without date, also Feb., 1905, Nov. 28, 1906, and May 11, 1907 (G. P. Goll). Department of Izabal: Puerto Barrios, Dec. 29, 1904 (Maxon and Hay); Quirigua (W. P. Cockerell). Los Amates, Feb. 7, 1905 (C. C. Deam) and (Kellerman); Bobas, May 24 (W. M. Mann).

HONDURAS: La Ceiba, March 19, 1916 (F. J. Dyer); Tegucigalpa, Oct. 30, 1917, and Aug. 11, 1918 (F. J. Dyer); Tela, on sweet potato (W. M. Mann); Guimas District, Tela, May 3, 1923 (T. H. Hubbell); Jilamo Farm, Tela, May 27, 1923 (T. H. Hubbell); Cecilia (W. M. Mann); Lombardia (W. M. Mann); Progreso, March, 1923 (T. H. Hubbell); El Canal, Puerto Castilla, March 28, 1924 (J. Bequaert); Corocito, April 3, 1924 (J. Bequaert); Prieta, April 6, 1924 (J. Bequaert); Cantarranas, Río Choluteca, 2200 feet, Sept. 5, 1930 (Honduras Exped. of Academy of Natural Sciences of Philadelphia); Lancetilla, Sept. 1, 1931 (D. M. Bates) and (R. E. Stadelmann); Subirana Yoro, Jan. (R. E. Stadelmann).

NICARAGUA: San Marcos (Baker); Escondido River, 50 miles from Bluefields, July (C. W. Richmond); Edén, 14° N. 84° 26' W., April 17, 1922 (Wharton Huber); Chontales (Janson).

COSTA RICA: Guápiles, March 8, 1903, and June 18, 1903 (J. C. Crawford); Port Limon, Sept. 28 and Sept. 30, 1905 (F. Knab); San Mateo; Zent, March, 1924 (H. W. Atkinson); Navarro Farm, April, 1924 (W. M. Mann); Orotina, May 6-7, 1924 (J. C. Bradley); Suretka, May 31, 1924 (F. R. Swift); Cache (H. Rogers); Pozo Azul de Perris, 325-550 feet, Aug. 21, 1926 (Lankester and Rehn); Hamburg Farm, July 26, 1937 (F. Nevermann), Dec. 7, 1937 (F. Nevermann).

PANAMA: Río Boqueron, May, 1907 (A. Busck). Province of Bocas del Toro: Changuinola District; Almirante (J. B. Smith). Province of Chiriquí: Progreso, April 21, 1923 (F. M. Gaige); Bugaba (W. Schaus); Bugaba, 800 to 1500 feet (Champion).

ECUADOR: Cachabi, Nov., 1896 (Rosenberg); Ecuador, 1000-2000 feet (E. Whymper); Bucay, 1000 feet, Oct. 10, 1922 (F. X. Williams); Naranjapata, 1850 feet, Dec., 1922 (F. X. Williams), and Nov., 1926 (W. J. Coxey).

Trigona (Trigona) ruficrus (Latreille)

"Arapuá," COELHO DE SCABRA, 1799, pp. 99-104.

Apis ruficrus LATREILLE, 1804b, pp. 176-177, pl. 13, fig. 12.

Melipona citriperda ILLIGER, 1806, p. 158.

Trigona ruficrus, JURINE, 1807, p. 246 (misprinted 146).

Trigona ruficrus, LATREILLE, 1809, p. 183.

Trigona ruficrus, LATREILLE, "1811"b, p. 293, pl. 20, fig. 5.

Melipona ruficrus, LAMARCK, 1817, p. 53.

Melipona (Trigona) ruficrus, LEPELETIER, 1825, p. 710.

Trigona ruficrus, PERTY, 1833, p. 26.

Melipona ruficrus, LAMARCK, 1835, pp. 272-273.

Melipona ruficrus, LEPELETIER, 1836, p. 426.

Melipona ruficrus, HALIDAY, 1837, p. 321.

Trigona ruficrus, SAY, 1837, p. 415.

Trigona ruficrus, ERICHSON, 1841, p. 219.

Trigona luteipes F. SMITH, 1854, p. 410.

? *Trigona ruficrus*, JARDINE, 1859, pl. 27, fig. 2.

Trigona ruficrus, SAY, 1859, p. 788.

Trigona ruficrus, F. SMITH, 1863a, p. 509.

Trigona ruficrus, F. SMITH, 1866, p. 326.

Trigona ruficrus, F. SMITH, 1868, pp. 133-134.

Trigona ruficrus, WOOD, 1874, fig. 288.

Trigona ruficrus, H. MÜLLER, 1875b, p. 43.

"Arapua," RAVERET-WATTEL, 1875, pp. 737, 738, 740.

Trigona ruficrus, GIRARD, 1876a, p. 193.

"Arapuá," ANONYMOUS, 1878a, pp. 73-74.

"Arapua," ANONYMOUS, 1878b, p. 74.

Trigona ruficrus, ROTHSCCHILD, 1878, p. 120, fig. 100.

Trigona ruficrus, KIRBY, 1884, p. 413.

Trigona ruficrus, H. VON IHERING, 1886, pp. 184-185, 187, pl. 1, fig. 5.

Trigona ruficrus, HOLMBERG, 1887, p. 276.

? *Trigona ruficrus*, DU BUYSSON, 1892, p. 54 (identified by J. M. Pérez).

Melipona ruficrus, PECKOLT, 1893, p. 580.

Melipona ruficrus, PECKOLT, 1894, pp. 88, 223-225.

"Irapoa" or "Caraboshá," AMBROSETTI, 1895, p. 699.

Trigona ruficrus, GRIBODO, 1895, pp. 200-201.

Trigona ruficrus variety *concolor* GRIBODO, 1895, p. 201.

Melipona luteipes, DALLA TORRE, 1896, p. 580.

Melipona ruficrus, DALLA TORRE, 1896, p. 583.

Trigona (Melipona) ruficrus, WASMANN, 1900b, p. 368.

Trigona ruficrus, SCHROTTKY, 1901, p. 216.

Trigona ruficrus, SILVESTRI, 1902b, pp. 134-137, text figs. 6-8, pl. 1, figs. 10, 13, 17, pl. 3, figs. 39, 40, 46.

Trigona ruficrus, BUTTEL-REEPEN, 1903a, p. 141, fig. 17.

Trigona ruficrus, BUTTEL-REEPEN, 1903b, fig. 17.

Trigona ruficrus, H. VON IHERING, 1903, pp. 184, 187, 228-231, 240, 242, 249, 255, 264, 266, 278, pls. 20, 21, 22, fig. 1.

Trigona ruficrus, GRÜNBERG, 1904, pp. 9, 10.

Trigona rufifrons, GRÜNBERG, 1904, pp. 14, 15.

Trigona ruficrus, H. VON IHERING, 1904b, pp. 382, 386.

"Irapuan," "Irapuan," "Arapua," H. VON IHERING, 1904b, pp. 379, 386.

Trigona ruficrus, WASMANN, 1904, p. 483.

Trigona luteipes, COCKERELL, 1905, p. 323.

Trigona ruficrus, BUTTEL-REEPEN, 1907, p. 468.

Trigona ruficrus, DUCKE, 1907, pp. 75, 89.

Melipona ruficrus, RUDOW, 1907, p. 30.

Trigona ruficrus, DUCKE, 1908b, p. 80.

Trigona ruficrus, STRAND, 1909, p. 235.

Trigona ruficrus, DUCKE, 1910a, p. 108.

Trigona ruficrus, DUCKE, 1910b, p. 368.

Trigona ruficrus, STRAND, 1910, pp. 557-558.

Trigona ruficrus (?) *rufoides* STRAND, 1910, pp. 557-558.

Trigona ruficrus, MARIANNO, 1910b, pp. 18-21.

Trigona ruficrus, MARIANNO, 1910d, p. 8.

Trigona ruficrus, BERTONI, 1911, p. 142.

Trigona ruficrus, MARIANNO, 1911, pp. 8, 13, 21, 24, 25, 32, 39, 40, 44, 50, 51, 53, 124-129, 136.

Trigona ruficrus, H. VON IHERING, 1912, p. 2.

Trigona ruficrus, COCKERELL, 1912b, p. 60.

? *Trigona ruficrus*, COCKERELL, 1913a, p. 12.

Trigona ruficrus, WHEELER, 1913, p. 7 (identified by T. D. A. Cockerell).

Melipona ruficrus, RUDOW, 1914, pp. 240-241, fig. 8.

Trigona ruficrus, SCHROTTKY, 1914, pp. 218-219.

Melipona ruficrus subspecies *ruficrus*, DUCKE, 1916, pp. 15, 24, 26, 27, 44, 129, 130, pl. 6, fig. 20.

Trigona ruficrus (sic), BERTONI, 1918, p. 224.

Trigona ruficrus, LUTZ AND COCKERELL, 1920, pp. 500-501 (except probably specimens from Zacapa, Guatemala, vide *Trigona* (*Trigona*) *corvina* Cockerell).

Trigona ruficrus, BOUVIER, 1921, p. 210.

Trigona ruficrus variety *concolor*, HERBST, 1921, p. 102.

Trigona ruficrus, PHISALIX, 1922, p. 428.

Trigona ruficrus, LUTZ, 1924a, pp. 205, 207, 210, 216.

Trigona ruficrus, BERLESE, 1925, p. 824.

Melipona ruficrus, BRISTOWE, 1925, pp. 479, 486.

Melipona ruficrus subspecies *ruficrus*, DUCKE, 1925, pp. 340, 341, 344, 346, 354, 370, 418-419, text fig. X, pl. 4, fig. 20.

Trigona ruficrus, BOUVIER, 1926, p. 39.

Melipona ruficrus, BISCHOFF, 1927, pp. 287, 290, 291, 293, fig. 121.

Trigona ruficrus, WHEELER, 1928, p. 251.

Trigona ruficrus, SALT, 1929, pp. 453, 461 (identified by H. F. Schwarz).

Melipona ruficrus, ALFKEN, 1930b, p. 9.

Trigona ruficrus (sic), L. MARTIN, 1930, p. 97.

"Irapuan," GUENTHER, 1931, pp. 297, 376.

Melipona ruficrus, ALFKEN, 1932b, p. 306.

Trigona ruficrus, SCHWARZ, 1932a, pp. 253, 256.

Trigona ruficrus, MAIDL, 1934, pp. 164, 177, 191, 316, 318, 568, 571, 572, 576, 577, 581, 583, 589, figs. 78, 79.

Melipona ruficrus, COSTA LIMA, 1936, p. 382.

Trigona (*Trigona*) *ruficrus*, SCHWARZ, 1938, pl. 53, figs. F, I.

Trigona ruficrus, R. VON IHERING, 1939, p. 75.

Trigona ruficrus, R. VON IHERING, 1940, pp. 402-403, 880.

"Arapuá," R. VON IHERING, 1940, p. 403.

Trigona (*Trigona*) *ruficrus*, MOURE, 1944b, p. 1.

Trigona ruficrus, SCHWARZ, 1944, p. 417.

Melipona ruficrus subspecies *ruficrus*, DUCKE, 1945, pp. 14, 22, 23, 36, 98-99, pl. 6, fig. 20.

Trigona ruficrus, LE COINTE, 1945, pp. 163-164.

WORKER

DIAGNOSTIC CHARACTERS: Black except for the almost invariably fulvous to ferruginous hind tibiae. Mandible five toothed, for the most part reddish, but with the basal half sometimes invaded or replaced by black. Length of malar space about the width of the flagellum. Width of clypeus at its greatest a little more than twice the length of clypeus. Clypeus characterized especially by a rather distinct median longitudinal fossa, with the region on each side of it thrown into prominence by the difference of level. Erect black hairs on clypeus and supraclypeus abundant, also present on scape. Hind tibiae with an inwardly placed angle posteriorly at apex.

HEAD: Black or mainly black. The facial quadrangle wide, the distance between the compound eyes at the level just below the middle ocellus about equal to the distance between the middle ocellus and the apex of the clypeus. The compound eyes fairly strongly convergent below, the distance that separates them at their level of greatest approximation (below) being about as 7 is to 8.5 when compared with their divergence at the level just below the middle ocellus. The clypeus raised somewhat above the level of the sides of the face and characterized particularly by a rather conspicuous fossa down its middle that gives the region on each side of the fossa a slightly swollen appearance. The width of the clypeus, measured from one

apico-lateral extremity to the other, a little more than twice its length; the apico-lateral extremities separated each from the nearest eye by about one-half the width of the flagellum. The supraclypeus about as prominent as the clypeus. The labrum simple. The mandibles (fig. 25) armed with five teeth. The length of the malar space, measured from the lower extremity of the eye to the middle of the base of the mandible, about equal to

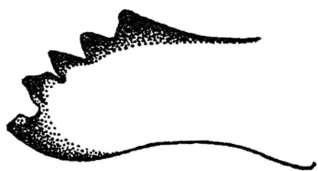


FIG. 25. Mandible of worker of *Trigona* (*Trigona*) *ruficrus* Latreille. Drawing by Alice Gray.

the width of the flagellum. The distance between the lateral ocelli a little less than that separating each lateral ocellus from the nearest compound eye. The carina behind the ocelli fairly well developed but somewhat blunt. Clypeus, front, vertex, and lower one-third of genal area more or less moderately shiny; the fine, appressed, silvery gray, microscopic hairs are usually rather dense on the sides of the face but are often rather inconspicuous on the clypeus and front; the upper two-thirds of the genal area silvery gray pruinose, or, held at certain angles, a little yellowish to olivaceous, especially towards the summit of the eye. All the other hairs of the head erect and black except usually at least some of those fringing the lower margin of the mandible, especially towards the apex of the mandible, which tend to be reddish to copper colored. Erect black hairs are present on the clypeus, supraclypeus, labrum, scape, front, vertex, and lower one-third of genal area, while in some specimens there are also short black hairs interspersed among the dense silvery gray appressed hairs of the upper two-thirds of the genal area. The black hairs rather abundant on clypeus and supraclypeus, for the most part exceeding in length those on the scape, although shorter than those towards the upper part of the front, which in turn are shorter than those of the vertex or of the inferior margin of the mandibles. The man-

dibles for the most part reddish but with the apical teeth black and sometimes with the basal half invaded or replaced by black. The labrum usually reddish, rarely black. The clypeus usually entirely black, with little or no red. The antennal sockets ferruginous; the scape usually entirely black, or black with a faint reddish stripe in front; the flagellum dark above and usually more or less ferruginous to brownish below, occasionally much clouded.

THORAX: Black, of rather subdued sheen due to the presence of grayish (in some lights occasionally brownish) tomentum on the thorax above, pleura, and sides of propodeum in addition to the longer, more conspicuous, but sparser simple black hairs in these areas. The relative length of the hairs as indicated in the description of the subgenus *Trigona*.

LEGS: The fore and middle legs, with the exclusion of the usually more or less ferru-

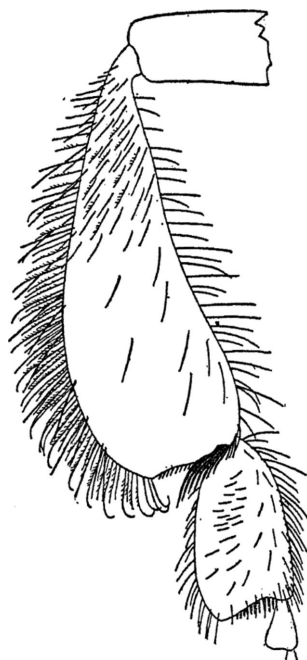


FIG. 26. Hind tibia and metatarsus of worker of *Trigona* (*Trigona*) *ruficrus* Latreille. Drawing by Elena Feld.

ginous small joints of the tarsi, black or reddish black, and the three basal joints of the hind tibiae similarly dark, but the hind tibiae (fig. 26) and tarsi, in contrast, almost

invariably of a ferruginous to fulvous color, rarely partly or wholly black (variety *concolor* Gribodo). The hind tibiae wider at the apex than at the base, clavate in outline; their anterior lateral contour gently emarginate; their posterior lateral contour more strongly convex; their apex with an inconspicuous angle anteriorly that bears the comb, this followed by a bulge in the apical contour that in turn is succeeded by an emargination; where this emargination terminates by running into the posterior contour, there is a somewhat inwardly placed angle. The outer face of the hind tibiae very gently arched anteriorly over approximately its basal two-thirds, somewhat flattened posteriorly and depressed on roughly its apical one-third. The flattened area constituting the posterior part of the under side of the hind tibiae about one-third of the width of the joint towards the apex. The hind metatarsi about three-fifths as wide at their widest (near the apex) as the hind tibiae are wide at their widest, the posterior apical angle being rather blunt to slightly acute. The hairs of the legs predominantly black but with the following relatively minor exceptions: the plumose hairs intermixed with the black simple hairs on the external face of the middle tibiae and extending usually to the basal part (especially posteriorly) of the associated metatarsi dark grayish to blackish; the plumose hairs fringing the hind tibiae posteriorly variable, inclined to be dark in the rare cases when the hind tibiae are dark but usually of lighter hue, grayish to light brown when these tibiae present the usual condition of being ferruginous to yellowish; the microscopic but stubby hairs on the elevated part of the under side of the hind tibiae and adjacent apical part beneath of the hind femora silvery gray; the suboval sericeous patch at base of under side of hind metatarsi silvery gray to whitish but frequently discolored by adherent foreign matter and in such cases often fulvous; the metatarsal brushes golden to copper colored. The relative length of the hairs and their distribution as indicated in the description of the worker of the subgenus *Trigona*.

WINGS: Dark. When the forewing overlays the hind wing, the brown is so intensified that the median cell and the adjacent areas

of the base of the wing seem almost of diluted iodine stain. The apical part of the wing a somewhat lighter grayish brown but without sharp transition. The upper one-half of the first transverse cubital vein and the entire second transverse cubital vein usually rather strongly demarked. The first discoidal cell about three-fourths as long as the marginal cell. Number of hamuli on each hind wing usually five, rarely four or six. Of 140 wings examined, 121 had five hamuli, 15 had six hamuli, four had four hamuli, an average of 5.08. The tegulae black or blackish.

ABDOMEN: Black or blackish, usually more or less telescoped, trigonate, about as wide as the thorax. Tergite 2 rarely with a very few shallow scattered punctures over its shiny surface and this tergite also with a narrow band of dense, appressed, dark, microscopic hairs; tergite 3 with a somewhat wider band of similar hairs including a few minute erect hairs, the hirsute area on this as on the previous tergite faintly tessellated; the subsequent tergites with short erect black hairs over their exposed surface, the chitin being slightly granular where these hairs emerge but otherwise smooth. Approximately the apical one-half of the several sternites with erect black hairs at the middle, these hairs grading into shorter hairs or sericeous patches on each side; these patches have sometimes a dark and sometimes a grayish sheen, depending on the specimen as well as the angle from which it is viewed. When the abdomen is telescoped, the hair bands form a continuous hairy surface. The tomentum on sternite 6 sometimes pale rather than black and the erect hairs few on this sternite.

MEASUREMENTS: Length 5.5 (cases of rather extreme telescoping) to 6.5 mm.; width of thorax 2.25 to 2.5 mm.; length of forewing, including tegula, about 7.5 to 7.75 mm.

QUEEN¹ (GRAVID)

HEAD: About as wide as the mesonotum, emphatically narrower than the distance between the outer rim of one of the tegulae and the outer rim of the other. The facial quad-angle wide, the distance between the compound eyes at the level just below the middle

¹ Description based on a single specimen from Massaranduba-Blumenau, Brazil. The queen has likewise been described by Silvestri (1902b, pp. 134-135).

ocellus about equal to the distance separating the middle ocellus from the apical margin of the clypeus. The eyes barely convergent below, almost parallel sided, somewhat shorter than those of the worker (about nine-tenths as long) and distinctly narrower than in that caste. The eyes very finely, microscopically, and sparsely hairy. The clypeus very gently arched, and, as is the supraclypeus, slightly raised above the level of the sides of the face, of smooth surface, entirely lacking the median longitudinal groove or channel so characteristic of the clypeus of the worker. The width of the clypeus, measured from one apico-lateral extremity to the other, about twice its length. The labrum simple, rounded in apical contour, with a very indistinct tubercle barely evident at the middle of the apex. The mandible with five distinct teeth along its apex. The length of the malar space about one and one-half times the width of the flagellum and roughly one-fifth to one-sixth as long as the eye. The ocelli small and remote from the eye, the distance from the summit of the eye to the nearest lateral ocellus being nearly twice that separating each lateral ocellus from the other. A low and blunt carina behind the ocelli. More or less moderately shiny are all parts of the head to the inclusion of the sides of the face and genal area, which, though covered with rather dense short hairs in addition to somewhat longer and sparser hairs, are not pruinose. The hairs on the head erect, rather coarse, and bristle-like, fully as abundant on the lower one-half of the face as on the upper half, and fuscous to here and there somewhat fulvous. The hairs on the under side of the mandible for the most part as long as, or longer than, the mandible is wide at the base and notably longer than those of the vertex; hairs also rather abundant over the outer face of the mandible. The hairs of the clypeus dense and about as long as those of the scape, which in turn have a length comparable to the width of the scape. The hairs increase in length towards the lower part of the genal area but even at their maximum are shorter than the hairs fringing the inferior margin of the mandible. The chitin for the most part black. The mandibles dull reddish on their apical one-third but not to the inclusion of the black apical teeth, and

there is some invasion of red on the clypeus. The flagellum, about twice as long as the scape, is (in the specimen on which this description is based) entirely bright ferruginous both above and below except for its dark first joint.

THORAX: Black, wider than that of the worker from the same nest. The length of the mesonotum plus scutellum a little greater than the width of the mesonotum at the base. Short tomentum present on the mesonotum, scutellum, and pleura, in addition to the longer, for the most part fuscous hairs, which attain their greatest length on the scutellum and on the thorax beneath. The middle area of the propodeum shiny and hairless.

LEGS: For the most part black or deep brownish, with the hind tibiae and tarsi more reddish but not so emphatically contrasted with the more basal joints and with the joints of the fore and of the middle legs as is the case in the worker from the same nest. Small tarsal joints of the fore and middle legs also more or less reddish. The hind tibiae barely longer than the hind trochanters plus femora, somewhat clavate in outline, their apex feebly rounded anteriorly and with a somewhat obtusely shaped angle posteriorly. The hind metatarsi about three-fifths as wide as the associated tibiae at the apex, and slightly tapering from near the base to the apex; the combined small joints of the hind tarsi about four-fifths as long as the metatarsi measured along the inner face; the inner face of the hind metatarsi uniformly covered with soft yellowish golden hairs rather even in length. Similar hairs are present on the inner face of the metatarsi of the fore and middle legs. The other hairs of the legs for the most part fuscous to black but grayish on the coxae, under side of trochanters (rather long, dense, and with a slightly yellowish sheen on the middle trochanters), under side of femora, outer face of metatarsi and small tarsal joints, and to some extent on outer face of hind tibiae. The femora are moderately hairy on their outer (anterior) and particularly under side, more glabrous on their inner (posterior) face. The hairs on the outer face of all the tibiae (including the hind pair) are relatively dense, and, although they tend to be progressively longer from the fore tibiae to the hind tibiae, the contrast in length

between those on the outer face of the fore tibiae and those on the outer face of the middle tibiae is much less emphatic than in the conspecific worker. Unlike the condition in the worker, no plumose hairs are intermixed with the simple hairs on the outer face of the middle tibiae and the adjacent region at base of middle metatarsi. The hairs along the posterior rim of the hind tibiae short and simple without clear trace of intermixed plumose hairs. The hairs fringing the several metatarsi along their posterior lateral contour distinctly longer than the hairs along the anterior lateral border or on the outer face of these joints.

WINGS: Smoky, shorter than in the worker, probably failing to reach the apex of the third tergite of the distended abdomen, although it is difficult to determine accurately their length owing to the frayed apex of the specimen before me. Tegulae rufo-fuscous. Number of hamuli not ascertainable because of fragmentation of lower wings.

ABDOMEN: Prevailing blackish. Tergite 1 almost glabrous, with only a few appressed hairs laterally along the apex; tergites 2 and 3 with moderately long, semi-erect, rather soft, and for the most part fuscous hairs apically and laterally, and tergite 3, at least, with two dense basal patches of very microscopic silvery gray hairs; tergites 4 to 6 with hardly any hairs as long as those in the apical region of tergites 2 and 3 and such hairs concolorous for the most part with the silvery gray microscopic hairs that are rather dense over most of the surface of these tergites. Where the hairs emerge, the surface appears punctate, finely so on tergites 4 to 6, more coarsely so on tergites 2 and 3. The erect hairs along the apex of the several sternites fuscous to fulvous; a fulvous tomentose area at middle of sternite 1 in addition to a few erect hairs.

MEASUREMENTS: Length about 9.5 mm. (of which the abdomen accounts for considerably more than one half); width of thorax about 2.75 mm. (Ducke, 1916, p. 130; 1925, p. 418; 1945, p. 98, gives the width of the thorax as 3.25 mm.); length of forewing, including tegula, about 7.5 mm., but because of the frayed apex, in the only specimen of the queen of *ruficrus* that is available, difficult to determine accurately.

MALE¹

HEAD: Black. The facial quadrangle not so wide as in the worker. The distance from one eye to the other at their level of greatest approximation near the lower extremity only about five-sevenths to three-quarters of the length of the eye, whereas in the worker the distance between the two eyes at the corresponding level is subequal to the length of the eye. The clypeus and supraclypeus raised only a little above the level of the sides of the face; the median longitudinal fossa of the clypeus less clearly demarked than in the worker; the apico-lateral extremities of the clypeus acute and barely separated from the compound eyes; the length of the clypeus a little more than half its greatest width. The labrum simple. The dentition of the mandibles very obscure; as Silvestri (1902b, p. 135) indicates, it is hardly traceable. In the specimen on which the present description is based a feebly bidentate condition due to a thickening of the chitin may be detected near the outer end of the apex if the insect is held at a certain angle, and there is a slight notch-like indentation near the middle of the apex; otherwise the inwardly receding apical edge has its surface uninterrupted, being virtually edentate. Unlike the mandible of the worker, which is largely red, that of the male is black except for a narrow red stripe just before the apex is reached. The malar space is rather shorter inwardly than the width of the joints towards the apex of the tapering flagellum. The distance between the lateral ocelli a little greater than that which separates each lateral ocellus from the nearest compound eye. The carina behind the ocelli fairly well developed but somewhat blunt. The head a little duller and somewhat more hirsute than that of the conspecific worker. The appressed silvery gray hairs fairly conspicuous on the clypeus and dense on the sides of the face and upper two-thirds of the genal area. Erect black hairs are present on the clypeus, scape, front, vertex, lower one-third of genal area, and fringing the lower edge of the mandibles. Those on the clypeus are longer than the hairs on the clypeus of the worker and longer

¹ Description based on a male from the State of Ceara, Brazil. The male is rare in collections. All the 500 to 600 specimens of this species examined by F. Smith (1866, p. 326) apparently were workers.

(especially those on the lower one-half of the clypeus) than the hairs on the scape of the male (the hairs of the scape approximating in length the width of the scape). There are minute erect black hairs, too, among the silvery gray appressed tomentum on the sides of the face and the genal area. The antennal sockets and the under side of the flagellum ferruginous.

THORAX: Black, of subdued sheen, especially on the mesonotum, due to the pres-

blackish with the following relatively inconspicuous exceptions: the tomentum of the under side of the trochanters dull grayish as are the plumose hairs of the outer face of the middle tibiae and the dense fringe of very microscopic hairs on the under side of especially the middle femora; the short bristles at the apex of the inner face of the hind femora and densely down the raised area of the inner face of the hind tibiae silvery gray as are the appressed sericeous hairs in the

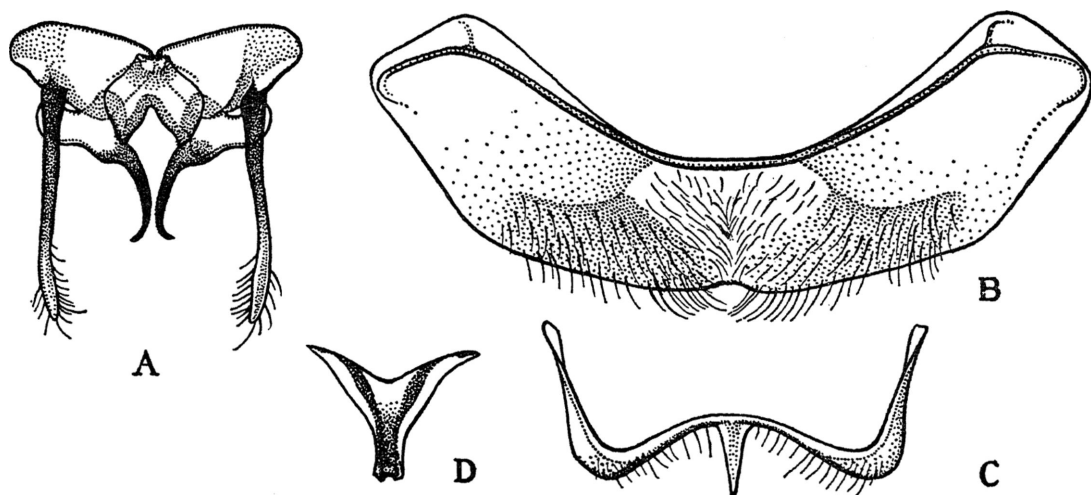


FIG. 27. Abdominal parts of the male of *Trigona (Trigona) ruficrus* Latreille. A. Genitalia (chitinized parts only). B. Sternite 5. C. Sternite 6. D. Sternite 7. All based on a specimen from State of Ceará, Brazil. Drawings by Shirley H. Risser.

ence of grayish tomentum, which is especially dense on each side of the polished middle region of the propodeum.

LEGS: Largely black except for the hind tibiae and hind metatarsi and tarsi, which in strong contrast are bright fulvous. Anterior lateral contour of the hind tibiae (fig. 38F) feebly concave; their posterior lateral contour much more strongly convex; their apical contour rounded; their outer face flattened posteriorly. The greatest width of the hind tibiae (near the apex) about five-sixths that of the hind tibiae of the worker at the corresponding level. The hind metatarsi towards the apex about three-fifths as wide as the associated tibiae; their posterior apical extremity subrectangular to rounded. The hairs of the legs predominantly black or

differentiated area at the base of the inner face of the hind metatarsi; the appressed hairs on the outer face (posterior half) of the hind tibiae and the dense fringe of hairs along the posterior lateral contour of these tibiae also approximately silvery gray; the metatarsal brush of at least the hind tibiae yellowish to reddish golden. The hairs fringing the posterior lateral contour of the hind tibiae densely and almost exclusively plumose, their length less than one-half the width of these tibiae. The distribution of the simple black hairs in general and their relative length approximately as indicated in the generalized description of the male of *Trigona*.

WINGS: As in the worker, smoky and with the upper one-half of the first transverse cubital vein and the entire second transverse

cubital vein rather clearly demarked. Number of hamuli five in the hind wings of the only male specimen before me.

ABDOMEN: Black or blackish, comparable in width with the thorax. The hairs of the tergites black; those of tergites 2 and 3 appressed, forming a narrow band along the apex; those of the subsequent tergites more erect; tergite 7 with a thin fringe of longish, incurved, black hairs and with short pale plumose hairs intermixed. For the structure of the sternites and genitalia, see figure 27.

MEASUREMENTS: Length 5.5 mm.; width of thorax 2.5 mm.; length of forewing, including tegula, 7.5 mm.

TYPE MATERIAL

There is in the Latreille collection at Oxford University a specimen marked "*Apis ruficrus* ouvrière." The handwriting corresponds with that on another specimen in the Latreille collection, and that handwriting a later commentator, probably Dejean or Serville, has designated "l'écriture de Latreille." There seems little doubt, therefore, that the insect in question is part of the type material. Another specimen at Oxford University that is likewise labeled *ruficrus* lacks the head, and it is not possible to be certain, therefore, whether this specimen shared with the first specimen the longitudinally channeled clypeus which I believe to be characteristic of *ruficrus*. In so far as its characters are evident, however, it seems to accord with the first specimen and is presumably also to be considered part of the type material.

The type material of *ruficrus* came from Brazil. From that country came also *luteipes* F. Smith, here interpreted as a callow of *ruficrus*. The type specimen of *luteipes* is in the British Museum (Natural History).

DISCUSSION

In many of the black species of *Trigona* subgenus *Trigona* the hind legs (and particularly the hind tibiae) are apt to be one of the last points of resistance in the transition from the callow to the dark, mature state. Specimens, the coloration of which is almost wholly black, will even in species other than *ruficrus* frequently have lighter-colored hind tibiae, but in *ruficrus* ferruginous to yellowish hind tibiae are with rare exceptions the rule.

Gribodo (1895, p. 201) named the form with dark tibiae *Trigona ruficrus* variety *concolor*, but it is open to question whether *concolor* is entitled to independent status. A series from Nova Teutonia, Brazil, includes examples of both *concolor* and typical *ruficrus*. There are also such melanistic specimens from Araraquara, Brazil, and from San Bernardino, Paraguay.

More fundamental than the coloration of the tibiae is the structure of the clypeus. In no other five-toothed *Trigona* is there so defined a median longitudinal channel bisecting the clypeus, with the result that the surface of the clypeus on each side of the channel in extreme cases takes on the character almost of a subtubercular swelling.

Strand (1910, pp. 557-558), in listing various localities in Paraguay where *ruficrus* was secured, devoted a special paragraph of comment to six workers from Villa Morra that "can hardly be differentiated morphologically from *Tr. ruficrus* but which are of an entirely different coloration," being largely brown or dark brown with a nearly black, longitudinal band on the face, coextensive with a polished area, and with brownish yellow base of abdomen and hind tibiae and tarsi. He named them with some hesitation *rufoides*, at the same time suggesting that they might merely be callows of true *ruficrus*. Strand found the face, exclusive of the area covered by the median dark band, duller than is usual in *ruficrus*, and to a lesser degree this dullness was characteristic also of the mesonotum and even of the scutellum.

Structurally *luteipes* F. Smith (1854, p. 410), the type of which I have examined, agrees with typical *ruficrus*. At most it can take rank as a variety of *ruficrus*, but I am much more inclined to regard it as a callow of *ruficrus*. This conclusion is strengthened by the fact that, in commenting on *ruficrus* some 12 years after he had described *luteipes*, Smith (1866, p. 326) stated: "One circumstance is noticeable. The mature bee is entirely black; but among the multitudes of specimens were found individuals of every shade of color between pale testaceous and black." Such a diverse aggregate of callows might well have included a specimen approximating the mainly "pale testaceous" *luteipes* in appearance. Peckolt, too (1894,

p. 223), mentioned great diversity of coloration among the "younger individuals" of *ruficrus*.

The length of the forewing, including the tegula, varies from 7.5 mm. to 7.75 mm. The specimens of shortest wing length are from San Bernardino, Paraguay, while specimens from Niotheroy, State of Rio de Janeiro, Brazil, attain the maximum length.

It is curious that several competent students of stingless bees have failed to discern that *ruficrus* is structurally distinct. Marianno (1911, p. 8) wanted to make *hyalinata* merely a subspecies of *ruficrus*, while Ducke, (1916, pp. 130-134; 1925, pp. 418-421; 1945, pp. 98-101) thus subordinated not only *hyalinata* and what are regarded here as some of the varieties of *hyalinata*, but actually *amalihea* (as here interpreted) as well.

Schrottky (1914, pp. 218-219) expressed the opinion that *ruficrus* is not separable specifically from *amalihea*, being merely a form of the latter. He even reported having obtained both forms from the same nest. Possibly, but it seems to me far more likely that the identification was incorrect and that what were interpreted as *ruficrus* were merely callow specimens of *amalihea* with hind legs incompletely colored, recalling the condition in *ruficrus*. If this explanation be found invalid, then I should be inclined to believe that the *ruficrus* part of the population was intrusive, not a natural part of the nest, for *ruficrus* is one of the most aggressive members of the stingless bees. Certainly it is structurally quite distinct from *amalihea*.

According to Peckolt (1894, p. 224), *ruficrus* is not at all "choosy" in selecting a nest site: "They dwell on trees in the primeval forest and in gardens, under the projecting roofs of houses, in hollow trees and beams." However, although Peckolt mentioned tree hollows as nesting sites, he also indicated that, although hollow boxes and hollow logs were made available by him to induce swarming bees to settle, a swarm of *ruficrus*, neglecting all these attractions, chose instead the branch of a high *Mangifera indica*, erecting a nest (clearly an exposed one) that resembled the nest of a termite. Subsequently, however, a swarm (possibly a daughter swarm from the nest on the *Mangifera* tree) did accept the hospitality

of one of Peckolt's empty boxes, and at a later date a swarm from that box took possession of a neighboring box that had been deserted by a family of pigeons that had found the bees undesirable neighbors.

All the nests of *ruficrus* recorded by observers other than Peckolt have been nests established in the open as distinguished from concealed nests (pl. 6, fig. 3). On his trip through Misiones, Argentina, Silvestri (1902b, p. 135) noted that all nests of this species were attached to the branches of trees, and H. von Ihering (1903, pp. 228-229) in describing a nest mentioned that it was built in the limb of a tree, with the branches penetrating the nest. Rudow (1914, pp. 240-241) described and figured an exposed nest enveloping a limb. A relatively small exposed nest, 30 cm. by 40 cm., was observed also by Fiebrig in Paraguay (cited by Strand, 1909, p. 235). Silvestri gave the range of size of the ovoid nests he observed as 36 cm. to 60 cm., while the nest of maximum size examined by H. von Ihering (1903, pp. 228-230) measured 70 cm. in height by 49 cm. in diameter. This nest, as did a somewhat smaller nest (58 cm. high by 44 cm. in diameter) also examined by von Ihering, consisted of 15 tiers of brood combs. The number of cells, 6 mm. in height by 4 mm. in width, totaled 4400; the adult population approximated 5500 bees. Only two queen cells, 11 mm. by 9 mm., were present in this large nest in contrast to at least 10 to 12 in the somewhat smaller nest examined by von Ihering, but, as the count in the case of the smaller nest was based on a study of only half its circumference, it is von Ihering's calculation that the entire nest may have contained as many as two dozen royal cells. The royal cells observed were all located at the periphery of the combs. If the number of royal cells estimated by von Ihering to have been present in the smaller of the two nests he examined seems large, his figures nevertheless find support in the observation of Silvestri (1902b, p. 137), who in a nest consisting, as in that of von Ihering, of 15 combs found from one to two royal cells on the periphery of each of the combs. Marianno, whose account (1911, pp. 126-129) of the biology of *ruficrus* is particularly informing, gives the range of the number of combs in nests of this species as 13 to

16. The provision pots are more or less circular and small, 10 mm. or less to 15 mm. in diameter.

The nest observed by Fiebrig, above alluded to, had what was described as many entrances, and he wondered whether they had been completed.

In the construction of its nest, particularly of the involucre of the nest, *ruficrus* employs among other things the excrement of herbivorous animals (never, according to Marianno, the excrement of Carnivora) and the excrement of cattle is particularly favored. But according to Marianno's observations (1910b, p. 19; 1911, p. 127) it is not the excrement in its entirety that is employed but merely the undigested bits of vegetable fiber, which the bee removes with its mandibles, aided by its fore legs.

Both H. von Ihering (1903, p. 229) and Marianno (1910b, p. 21; 1911, p. 127) mention a peculiar bowl-shaped structure in nests of *ruficrus* which von Ihering designated the scutellum and which is here reproduced as plate 6, figure 4. It is constructed preferably of mud and wax and finds place within the nest. Although nearly solid, it is penetrated here and there by irregular passageways, and these passageways, strangely enough, are filled with the bodies of dead bees of the hive. According to Marianno (1910b, p. 21), the older the nest, the larger the scutellum and (as a concomitant) the fewer the inhabitants of the hive. Ducke (1925, p. 418) states that the scutellum may occupy more than half of the nest, imparting stability to the structure. Unusually large was the scutellum in the spacious nest (70 cm. in height by 49 cm. in diameter) above referred to. Its bulk filled far in excess of half of the interior of the nest and contributed substantially to the inordinate weight of the structure (60 kg.).

Worthy of mention is the spiral arrangement of the combs, the axis, according to H. von Ihering (1903, p. 230), being located eccentrically.

It is claimed by R. von Ihering (1939, p. 75; 1940, p. 403) that the nest of this bee has toxic qualities and that along the San Francisco River in Brazil it is used effectively to poison the fish.

Frederick Smith (1866, p. 324) hazarded

the opinion, based on an examination of the nest material of *Trigona (Plebeia) mosquito*, which included one gravid and five virgin queens, that *Trigona* bees swarm "in the same manner as *Apis mellifica*." The swarming was subsequently confirmed by T. Peckolt, the donor of the nest of *mosquito*, with respect to *ruficrus*. F. Smith (1868, pp. 133-134) quoted Peckolt as follows:

"Your conjecture respecting the swarming of *Trigona Mosquito* is now confirmed; I made inquiry of several people, who told me they had observed the swarming of these bees, but I had never done so myself. I have, therefore, in consequence of your notice, obtained hives of three or four species, which I have established in my garden. I have also searched six separate hives, to see whether there was more than one female in each,—that is, one that was impregnated; and from your description, I had no difficulty in recognizing the queen; but I never could find more than one. I have now in my garden, one hive of *Trigona Mosquito*, one of *Trigona ruficrus*, one of *Trigona Mandaçaia*, and one of *Trigona Uruçu*. I very frequently watch them during the day, and have observed *Trigona ruficrus* swarm, just like the European honey-bees. This I have done about the end of March, when the cold time begins, whilst in April, May, June and July, they appear to increase very scantily, I suppose in order not to raise too many useless feeders. The first swarming that I observed occurred during a thunder-storm. A great number left their hive, with their queen, just as I have seen the honey-bee *Apis mellifica*, and indeed their mode of life appears to be almost identical."

The implication of Peckolt is that the new swarm sets forth, after the manner of the Old World honeybee, with the old gravid queen, leaving the continuation of the role of queen in the parental hive to her royal progeny.

However, this view is at variance with that expressed by Silvestri (1902b, p. 166) and H. von Ihering (1903, p. 181). The former indicates that the foundation of new colonies is the destiny of the virgin queens; the latter speaks of the "life-long confinement of the queen within the nest." This would seem almost necessarily to be the case, for the disproportionately large abdomen of the

gravid queen compared to her very small, often badly frayed wings, precludes the suggestion of flight and points to the probability that it is the virgin queens that participate in the dispersal flights of the species. Hockings (1884, p. 154) regarded queens of Australian *Trigona* as "quite incapable of flight when the ovaries are developed" and went on to say that they "even appear to walk with difficulty."

Later Peckolt (1894, p. 224) recorded a total of three acts of swarming of *ruficrus*. It is especially to be emphasized that all of them occurred in March and at the time of a thunder storm.

Hermann von Ihering (1912, p. 2) referred to *ruficrus* with a show of temper as a robber bee, a designation more frequently applied to *Lestrimelitta limão* (F. Smith), and accused *ruficrus* of "scandalous impertinence" in interfering with his experiments to start new colonies of stingless bees by artificially dividing a colony with fresh brood combs. A colony of *ruficrus*, according to von Ihering's observations (1903, p. 260), attacked several *Melipona* nests in turn and robbed them of their stored provisions. Silvestri (1902b, p. 137) found the attacks of *ruficrus* very savage, likening its pugnacity to that of species of the subgenus *Oxytrigona*, commonly rated the most unpleasant of stingless bees. H. Müller, too (1875b, p. 43), coupled *ruficrus* with *tataira*, an *Oxytrigona*, as one of the most aggressive of bees, and Peckolt (1894, p. 224) affirmed that not only does *ruficrus*, contrary to the behavior of all other stingless bees, fail to retreat when tobacco smoke is blown its way, but it is actually driven to fury by the act. Peckolt (1894, p. 224) and von Ihering noted not only the annoying viciousness of *ruficrus* but also its destructiveness to orchards, which is also confirmed by Marianno (1910b, p. 20; 1911, pp. 126, 129). Marianno mentioned as fruit trees that are attacked with especial ruthlessness the domestic fig (*Ficus carica*) and the orange. The leaf buds of various trees (particularly fruit trees) are bitten off by this bee, according to Peckolt (1894, p. 224). He included among the arboreal victims: orange trees, *Persea gratissima*, *Anona squamosa*, and *Schinus terebinthifolius*. Costa Lima (1936, p. 382) ob-

served this species gnawing the rind of *Citrus* fruit.

As a possible offset to its devastations, however, *ruficrus* is, according to Marianno (1911, p. 129), the natural agent of pollination of the banana, and Peckolt (1894, p. 224) found it particularly abundant on the flowers of this fruit. Peckolt (1894, p. 224) also stated that this bee was exceedingly partial to *Jatropha multifida*, the purple red blossoms of which were all but concealed by the black visiting bees. Strand (1909, p. 235) reported that Fiebrig had observed *ruficrus* on the flowers of a *Cassia* in Paraguay, and Costa Lima (1936, p. 382) mentioned A. Silva as having seen it attacking branches of *Cassia multijuga*. Alfken (1930b, p. 9), citing the field observations of Roman in the Brazilian State of Bahia, recorded this species as a probable visitor of one of the violet Compositae or of the lilac-colored *Convolvulus* flowers that grow in the region.

According to Marianno (1911, p. 128) *ruficrus* is partial to the latex and resins of certain indigenous and exotic plants, ravaging Euphorbiaceae, Papaveraceae, Terebinthaceae, and Urticaceae. But, not content with gathering the natural overflow of the prized products, *ruficrus* induces the flow by wounding the plant tissue with its strongly toothed mandibles. It has the habit, too (shared by some of the bumblebees, notably the North American *Bombus affinis* and *Bombus terricola*), of perforating the plant in order to arrive more quickly, if illegitimately, at the liquid sweets in the nectaries (Marianno, 1910b, p. 20; 1911, pp. 128-129).

Schrottky (1901, p. 216) noted that *ruficrus* nibbles the leaves of *Solanum paniculatum*, which, he emphasized, are covered over with a hairy growth. Perhaps such leaf fragments enter into the construction of the nest.

Peckolt (1894, p. 224) pronounced the honey of this bee disgusting and others have confirmed this impression. The honey of *ruficrus* H. von Ihering described as "blackish-brown, opaque, odorless, of unpleasant, nauseating, acridly sour taste, with strong acid reaction." According to Silvestri (1902b, p. 137) it is purgative.

It was von Ihering (1886, pp. 184-185) who, on the basis of his observations on

ruficrus, suggested the possibility of dimorphism among the workers of stingless bees, a subject discussed in the section on division of labor in the Introduction to the present paper (pp. 39-41).

According to Peckolt (1894, p. 223) *ruficrus* discharges a sticky fluid as she crawls about in the fur of animals or the hair of people. Sometimes, Peckolt declared, this proves her own undoing as she may herself become glued to the hairs. Because of this discharge and certain other fancied resemblances to members of the subgenus *Oxytrigona*, it was Peckolt's suggestion that these bees be retained in the genus *Trigona* at the same time that most other species described as *Trigona* be relegated to *Melipona*. Several other bees, including *tubiba*, were, however, to be retained with *ruficrus* in the *Trigona* group.

Bristowe (1925, pp. 479, 486) stated that a philanthid wasp, *Trachypus gomesii* Klug, which is common in banks near Rio de Janeiro, stores its nest with stingless bees, especially *ruficrus*.

Wasmann (1900b, p. 368; 1904, p. 483) reported the presence of adults and larvae of the beetle *Nausibius clavicornis* in nests of *Trigona ruficrus* collected by H. von Ihering in Rio Grande do Sul, Brazil.

The names by which *ruficrus* is popularly known in Brazil are: "arapuá," "arapoña," "arapica," "eira-apuá," "irapuá," "irapoan," and "irapuan." It is to the last name (of Tupi origin) that H. von Ihering (1904b, p. 382) and Marianno (1911, p. 124) gave preference, explaining that "ira" means bee and "puan" or "poan" means round, which is the general shape of the usually exposed nest that *ruficrus* builds. Guenther (1931, p. 297) indicated that "ira" is used in the sense of honey. Thus the combination "ira-puan" signifies round bee or round honey, an allusion to the shape of the nest of *ruficrus*, "which hangs on the bough of some forest tree like a great dark ball." It should be mentioned that two of the popular names applied to *ruficrus*, namely, "irapuan" and "arapuá," are used also for *Trigona (Trigona) hyalinata* Lepeletier (Ducke, 1916, p. 133; 1925, p. 344; 1945, p. 101). There is even a locality known as Arapuá in the Brazilian State of Matto Grosso, and that the place

may well have been named in honor of *ruficrus* seems to be indicated by the fact that specimens of this species have been collected there. There are also localities designated Arapuá in the Brazilian states of Ceará and Minas Gerais. Marianno (1910b, p. 18) indicated that the term "arapuá" is used in the State of Pernambuco, whereas "irapoan" is favored in the State of São Paulo. Yet another name for *ruficrus* is "abelha de cachorro," which, however, also designates *Trigona (Trigona) fulviventris* Guérin and its variety *guianae*. Ambrosetti (1895, p. 699) referred to "irapoa," an insect from the Alto Paraná, Misiones, as a wasp, but it would seem that he inferred it was a wasp because it built an exposed nest. An alternative name for "irapoa" in the Alto Paraná or Misiones area of Argentina is, according to Ambrosetti, "caraboshá," which is very similar to the name Carabozá that Silvestri (1902b, p. 134) recorded on a trip to that region. A Guarini name for this bee is "karavosá" (Bertoni, 1911, p. 142). Evidently the last three names are all very closely allied and may indeed be merely individual interpretations of the same spoken word.

DISTRIBUTION

The bee was described from Brazil, and all of the records with one exception are from South America. Wheeler (1913, p. 7) and Cockerell (1913a, p. 12) listed as typical *ruficrus* a *Trigona* from Zacapa, Guatemala, collected December 13, 1911. I have not seen the specimen in question, but the absence of any other records from Central America makes me wonder whether the instance reported was not a callow of *corvina*. Ducke (1916, p. 130; 1925, p. 419; 1945, pp. 98-99) reported the occurrence of typical *ruficrus* in the Brazilian States of Maranhão, Ceará, Bahia (from which it was recorded by Kirby, 1884, p. 413, and by Alfken, 1930b, p. 9), Minas Gerais, Rio de Janeiro, São Paulo, Santa Catharina, and Rio Grande do Sul. Cockerell (1912b, p. 60) listed it from the States of Rio Grande do Norte and Parahyba. Probably it is *ruficrus* that is referred to under the designation "arapuá" by Castello Bruneo in his account of the bees from the Brazilian State of Piahy (Anonymous,

1878b, p. 74). Alfken (1932b, p. 306) had specimens from the State of Pernambuco. From Brazil *ruficrus* extends across the border into Argentina, where Silvestri (1902b, p. 135) recorded it from Misiones, and also into Paraguay (Strand 1909, p. 235; 1910, p. 557; and Bertoni, 1918, p. 224). Du Buysson (1892, p. 54) recorded the species from Venezuela, but the identification (by Pérez) may be incorrect.

Gribodo (1895, p. 201) described what he designated *Trigona ruficrus* variety *concolor* from Parral, Chile. In summary Gribodo said: "Finally, a fact quite remarkable, is the discovery of two species of *Trigona* (*ruficrus* and *pallida*) in this subregion of the Neotropical fauna. As one has been able since several years to acclimatize a species of *Trigona* in France, it may be said henceforth that the existence of this genus has been demonstrated in all the zoological regions of our globe: in the domestic state in the Palaearctic region, in the wild state in other regions." Herbst (1921, p. 102) questioned the accuracy of Gribodo's locality designations for *ruficrus* and *pallida*, asserting that they "certainly were not obtained from southern middle Chile, 36°, and indeed not from Chile; this designation is based on a serious error. The deceased Edwyn C. Reed observed the Hymenoptera of Chile from Copiapó to Valdivia for forty years; I myself for twenty years in districts of varying geographic breadth, on the coast as well as in the mountains, and never, with the exception of the indigenous *Bombus dahlbomi* Guér. and the introduced *Apis mellifica* var. *ligustica* Spin., has there been found a social bee or a social wasp in Chile. The territory between Concepcion and Parral has been searched by me throughout several years intensively and methodically for Hymenoptera; nowhere in Chile has there thus far been revealed a trace of Meliponidae."

In the collections under consideration there are specimens from the following localities:

BRAZIL: State of Ceará: male as well as workers (Cornell Univ.); Mirim (W. M. Mann). State of Parahyba: Independencia (Mann and Heath). State of Pernambuco: Pernambuco (= Recife), Dec. 29, 1882; Escada, April, 1924 (F. X. Williams). State of Bahia: Bahia, May 25, 1915

(P. G. Russell), Machado Portela, June 6-20, 1915 (P. G. Russell); Toca da Onça, June 27, 1915 (P. G. Russell). State of Goyaz: Campinas (Cornell Univ.). State of Rio de Janeiro: Rio de Janeiro, Dec., 1856 (H. Clark) and (J. Gray), July, 1915 (P. G. Russell), Oct. 10, 1919 (Cornell Univ. Exped.); Nichteroy, Oct. 15, 1919 (Cornell Univ. Exped.); Tijuca, Oct. 17, 1919 (Cornell Univ. Exped.); Petropolis, Oct. 24-27, 1919 (R. G. Harris, Cornell Univ. Exped.); Alta Boa Vista, Oct. 30, 1919 (Cornell Univ. Exped.); Rezende, Feb., 1924 (F. X. Williams); Campo Bello, April 1-10, 1927 (A. Seitz). State of Minas Gerais: Tejuco (= Diamantina), Jan., 1857 (H. Clark) and (J. Gray); Uberaba, 1900 (Draenert); Bello Horizonte, Nov. 1-6, 1919 (Cornell Univ. Exped.); Lassance, Nov. 9-19, 1919 (Cornell Univ. Exped.); Viçosa, 1931 (Mrs. Y. Mexia). State of Matto Grosso: Arapuá; Aquidauana, Dec. 11-13, 1919 (Cornell Univ. Exped.). State of São Paulo: Jundiahy, Oct. 10, 1897 (Schrottky); Santos (A. Seitz); Araraquara, March 8-10, 1927 (A. Seitz); Rio Preto, March 12-14, 1927 (A. Seitz); Cayeiras, 1900 (Wingert); Igarassú; São Paulo, Feb. 16, 1912 (G. E. Bryant); Ypiranga (Cornell Univ.). State of Paraná: Rio Negro, July 15, 1936, and Oct. 24, 1936. State of Santa Catharina: Massaranduba-Blumenau, Sept.-Oct., 1935, queen and workers; Nova Teutonia, Sept. 27, 1939, Oct. 9, 1939, Oct. 18, 1939 (F. Plauermann). State of Rio Grande do Sul (R. von Ihering).

PARAGUAY: San Bernardino, June 12 (K. Fiebrig).

Trigona (*Trigona*) *corvina* Cockerell

Trigona ruficrus corvina COCKERELL, 1913a, p. 12.
? *Trigona ruficrus*, COCKERELL, 1913a, p. 12 (specimens from Zacapa, Guatemala).

Trigona ruficrus corvina, WHEELER, 1913, p. 7 (identified by T. D. A. Cockerell).

? *Trigona ruficrus*, WHEELER, 1913, p. 7 (specimens from Zacapa, Guatemala).

Trigona ruficrus corvina, COCKERELL, 1918d, p. 482.

Trigona ruficrus corvina, COCKERELL, 1920c, p. 465.

? *Trigona ruficrus*, LUTZ AND COCKERELL, 1920, pp. 500-501 (specimens from Zacapa, Guatemala).

Trigona ruficrus corvina, LUTZ AND COCKERELL, 1920, p. 501.

Trigona ruficrus corvina, COCKERELL, 1922, p. 8.

Trigona ruficrus corvina, LUTZ, 1924a, pp. 205, 210, 216.

Trigona ruficrus corvina, RAU, 1933, pp. 16, 36-37, 216 (identified by Grace Sandhouse and by H. F. Schwarz).

Trigona ruficrus corvina, SCHWARZ, 1934, pp. 4, 10.

Trigona ruficrus corvina, MAIDL, 1934, p. 164.

Trigona corvina, MICHENER, 1946, pp. 180, 190, 191, 192, 193-195 (identified by H. F. Schwarz).

WORKER

DIAGNOSTIC CHARACTERS: Black. Mandible five toothed, reddish to brownish over most of its surface. Length of malar space about equal to width of flagellum. Width of clypeus at its greatest a little more than twice length of clypeus. Clypeus gently arched with a very shallow median longitudinal fossa, in some specimens only faintly traceable. Black, erect hairs on clypeus so few and so short that they are easily overlooked; black bristles present on supraclypeus and

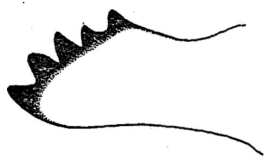


FIG. 28. Mandible of worker of *Trigona (Trigona) corvina* Cockerell. Drawing by Elena Feld.

scape. Hind tibiae with an inwardly placed angle at the apex posteriorly. Wings smoky.

HEAD: Black or mostly black. The facial quadrangle wide, the distance between the compound eyes at a level just below the middle ocellus about equal to the distance separating the middle ocellus from the apex of the clypeus. The compound eyes rather strongly convergent below, the distance that separates them at their level of greatest approximation (below) being about as 6.75 is to 8.25 when compared with their divergence at the level just below the middle ocellus. The clypeus rising somewhat above the level of the sides of the face; a longitudinal impress or fossa (less pronounced than in the nearly related *ruficrus*) down the middle of the clypeus, in extreme cases only faintly traceable. The width of the clypeus, measured from one anterolateral extremity to the other, a little more than twice its length; the anterolateral extremities separated each from the nearest compound eye by less than the width of the flagellum. The supraclypeus fairly prominent. The labrum simple, rounded to

triangular along apex. The mandibles armed with five teeth (fig. 28). The malar space, measured from the base of the mandible at its middle to the nearest point on the eye, about as long as the flagellum is wide. The distance between the lateral ocelli a little less than that between a lateral ocellus and the nearest compound eye. A blunt low to moderately developed carina behind the ocelli. Clypeus, supraclypeus, front, vertex, and lower one-third of genal area more or less moderately shiny. The sides of the face and particularly the upper two-thirds of the genal area silvery gray pruinose (now and then a little yellowish in some lights, especially towards the summit of the eye); the clypeus and the front somewhat less densely covered with appressed silvery gray microscopic hairs, those on the clypeus frequently worn off in part. The erect hairs black except as otherwise noted. Those of the clypeus very few and distinctly short, contrasting with the relatively long and abundant black hairs on the clypeus of *ruficrus*; usually the black hairs on the clypeus of *corvina* are so few as to be overlooked and are of shorter length than the erect black hairs on the scape. Erect hairs also on the supraclypeus and in other regions of the head mentioned in the description of the subgenus *Trigona*, those fringing the lower edge of the mandibles varying from black, like the other hairs, to copper colored. The mandibles reddish to brownish, with the basal prominences and the apical teeth black. The labrum sometimes a little reddish (as is at times also the clypeus) but in other cases wholly black. The antennal sockets ferruginous. The flagellum usually blackish above, brownish below, with sometimes a dull brownish stripe in front on the otherwise black scape.

THORAX: Black or blackish, of somewhat subdued sheen due to the presence of dull gray to light brownish tomentum on the mesonotum, scutellum, and mesopleura, in addition to the longer, more conspicuous but sparser simple black hairs in these regions. The sides of the propodeum with dull, silvery gray tomentum interspersed with erect black hairs. The relative length of the thoracic hairs as indicated in the description of the subgenus *Trigona*.

LEGS: Black to sometimes more or less

brownish black or reddish black, with the apical joint of the tarsi tending to be usually somewhat reddish; the hind legs (unlike the usual condition in *ruficrus*) not emphatically contrasted in color with the fore and middle legs; where approximations to a much lighter coloration in the hind tibiae and metatarsi occur, the specimen shows other evidences of being a callow. The hind tibiae (fig. 29) clavate, wider at the apex than at the base; their anterior lateral contour feebly concave; their posterior lateral contour strongly convex; their apical contour with an inconspicuous angle anteriorly that bears the comb, followed by a slight bulge, which in turn is succeeded by an emargination and finally by a well-defined, somewhat inwardly placed angle where the apical contour joins the posterior contour; the outer face of the hind tibiae gently arched anteriorly and basally but flattened to slightly hollowed on its apical one-third, particularly posteriorly. The flattened area constituting the posterior part of the under side of the hind tibiae about one-third of the width of the joint towards the apex. The hind metatarsi a little more than one-half as wide at their widest (near the apex) as the hind tibiae are wide at their widest (a little before the apex), the posterior apical angle of the hind metatarsi not acute but rounded to rectangular. The hairs of the legs black predominantly but with the following relatively minor exceptions: the plumose hairs intermixed with the black simple hairs on the external face of the middle tibiae and extending usually to the basal part (especially posteriorly) of the associated metatarsi dark grayish to brownish, and this, too, is usually the coloration of the plumose hairs fringing the hind tibiae posteriorly; the microscopic but stubby hairs on the elevated part of the under side of the hind tibiae and adjacent apical part beneath of the hind femora silvery gray; the suboval sericeous patch at base of under side of the hind metatarsi silvery gray but frequently discolored by adherent sticky matter; the metatarsal brushes copper colored (sometimes appearing black if viewed from a certain angle). The relative length of the hairs and their distribution as indicated in the description of the worker of the subgenus *Trigona*.

WINGS: Moderately and more or less

uniformly smoky, with usually fuscous to sometimes amber-colored venation and stigma. The upper one-half of the first transverse cubital vein and the entire second transverse cubital vein demarked with somewhat vari-

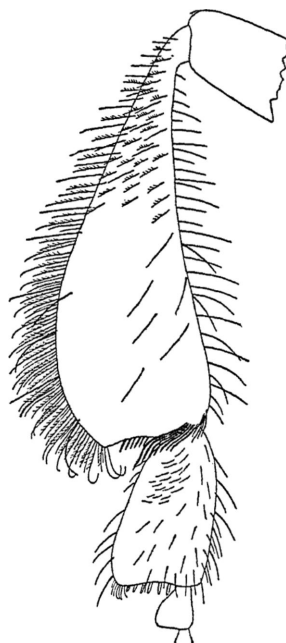


FIG. 29. Hind tibia and metatarsus of worker of *Trigona (Trigona) corvina* Cockerell. Drawing by Elena Feld.

able intensity, sometimes feeble, in other cases fairly strong. The first discoidal cell nearly three-fourths as long as the marginal cell. The number of hamuli per lower wing usually five, rarely six, very rarely four or seven. Of 250 wings examined, 225 had five hamuli, 18 had six hamuli, five had four hamuli, two had seven hamuli, an average of 5.07. The tegulae rufo-piceous to black.

ABDOMEN: Black or blackish, usually more or less telescoped, fairly compact, trigonate, comparable in width with the thorax. Tergite 2 with often a very few sparse shallow punctures on its polished surface and with a narrow band of appressed dark microscopic hairs along its apex, which is very faintly tessellated; a similar but slightly wider hirsute band on tergite 3 which, in addition to the appressed hairs, has erect black hairs that are succeeded by longer and more conspicuous black hairs on the exposed parts of the

subsequent tergites. Where these erect hairs emerge, the otherwise smooth surface of the tergites is faintly roughened to slightly granular. Approximately the apical one-half of the several sternites with erect black hairs at the middle which grade into sericeous patches at each side. These patches have sometimes a dark, at other times a grayish sheen, depending on the specimen as well as the angle from which the abdomen is viewed. When the abdomen is telescoped, the hair bands form a continuous hairy surface. The tomentum on sternite 6 tends to be pale, and the erect hairs on this sternite are few.

MEASUREMENTS: Length 4.75 to 5.5 mm.; width of thorax 2 to 2.25 mm.; length of forewing, including tegula, 6.75 to about 7.25 mm.

QUEEN (VIRGIN)¹

HEAD: About as wide as the mesonotum, distinctly narrower than the distance between the outer rim of one of the tegulae and the outer rim of the other. The facial quad-angle wide, the distance between the compound eyes at the level just below the middle ocellus about equal to the distance separating the middle ocellus from the apical margin of the clypeus. The eyes only slightly convergent below, somewhat shorter than those of the worker (about nine-tenths as long) and distinctly narrower. The eyes sparsely supplied with very microscopic fine pale hairs that can be detected only when the insect is viewed from a favorable angle. The clypeus gently arched and, as is the supraclypeus, slightly raised above the level of the sides of the face, of smooth surface, but with a faint longitudinal fossa down its middle (it is open to question whether this character is not subject to variation just as it tends to vary in the worker). The width of the clypeus, measured from one apico-lateral extremity to the other, about twice its length. The labrum with an indistinct tubercle barely evident at the middle of the apex. The outermost tooth of the quinquedentate mandible long, the second distinctly short, notably shorter than the third and completely dwarfed by the outermost tooth. The length of the malar space about one and one-half times the width of the

flagellum and roughly one-fifth to one-sixth as long as the eye. The ocelli small and remote from the eye, the distance from the summit of the eye to the nearest lateral ocellus being a little less than twice that separating each lateral ocellus from its fellow. The carina behind the ocelli low and blunt. The head more or less moderately shiny, somewhat dulled over the sides of the face and the genal area, the latter not pruinose. The hairs erect, rather coarse, and bristle-like, fully as abundant on the lower one-half of the face as on the upper half, almost wholly black, but rather conspicuously bright red on the outer face of the mandible near its apex and here and there copper colored on the fringe along the lower edge of the mandible. The hairs of this fringe are for the most part as long as, or longer than, the mandible is wide at the base and notably longer than the hairs of the vertex. The hairs of the clypeus dense and about as long as those on the inner side of the scape, which approximate in length the width of the scape. The hairs a little longer on the supraclypeus than on the clypeus. Short but increasing in length upward on the front, they attain on the vertex a length comparable with that of the hairs of the supraclypeus. The hairs increase in length towards the lower part of the genal area but even at their maximum are very notably shorter than the hairs fringing the mandible below. The chitin for the most part black but the mandible with a bright red band near the apex (just behind the black apical teeth); the antennal sockets ferruginous, and the flagellum, which is about twice as long as the black scape, entirely bright ferruginous.

THORAX: Black, wider than that of the worker from the same nest. The length of the mesonotum plus scutellum barely greater than the width of the mesonotum at the base. Short tomentum present on mesonotum, scutellum, and pleura in addition to the longer black hairs, which attain their greatest length on the scutellum and on the thorax beneath. The middle area of the propodeum shiny and hairless.

LEGS: For the most part black, but the small tarsal joints of all the legs and the anterior half of the outer face of the hind tibiae and metatarsi reddish. The hind tibiae a trifle longer than the hind trochanters plus

¹ Description based on two specimens from Juan Mina, Canal Zone.

femora, somewhat clavate in outline, their apex rounded anteriorly and with a somewhat obtusely shaped angle posteriorly. The hind metatarsi about three-fifths as wide as the associated tibiae at the apex, and very slightly tapering from near the base to the apex; the combined small joints of the hind tarsi about four-fifths as long as the metatarsi measured along the inner face; the inner face of the hind metatarsi uniformly covered with golden hairs that are rather even in length. Golden hairs cover also the inner face of the fore and middle metatarsi. The other hairs of the legs for the most part black. The femora with some hairs on their outer (anterior) side and on their under side, glabrous on their inner (posterior) face. The hairs on the outer face of all the tibiae (including the hind pair) are relatively dense, and, although they tend to be progressively longer from the fore tibiae to the hind tibiae, the contrast in length between those on the outer face of the fore tibiae and those on the outer face of the middle tibiae is much less emphatic than in the conspecific worker. Unlike the condition in the worker, no plumose hairs are intermixed with the simple hairs on the outer face of the middle tibiae and the adjacent region at the base of the middle metatarsi. The hairs along the posterior rim of the hind tibiae short and simple, without trace of intermixed compound hairs. The hairs fringing the several metatarsi along the posterior lateral margin much longer than those along the anterior lateral border or on the outer face of these joints.

WINGS: Moderately smoky, actually longer than in the worker from the same nest but not, as in the worker, extending beyond the apex of the abdomen. Tegulae rufo-fuscous. Number of hamuli, in the four wings examined, five.

ABDOMEN: Prevailing blackish. Tergite 1 largely glabrous, the few hairs short and located for the most part at each side, especially near the apex. The exposed parts of tergites 2 to 6 rather uniformly and densely covered with soft, non-bristle-like hairs, those on tergites 2 and 3 and in some positions also 4 blackish, those on tergites 5 and 6 grayish. Where the hairs emerge, the surface appears punctate, more coarsely so on tergites 2 and 3, more finely so on tergites

4 to 6. A tomentose area at the middle of sternite 1 in addition to the erect apical hairs; the erect hairs along the apex of sternites 2 to 5 blackish. The hairs on sternite 6 mostly short and pale but fulvous at the apex of this sternite.

MEASUREMENTS: Length 8.5 mm.; width of thorax 2.75; length of forewing, including tegula, about 8 mm.

MALE

HEAD: Black. The facial quadrangle narrower than in the worker. The distance from one eye to the other at their level of closest approximation (near the apex) about five-sevenths the length of the eye, whereas in the worker the distance separating one eye from the other at the level of maximum convergence is almost equal to the length of the eye. The clypeus and especially the supra-clypeus raised well above the level of the sides of the face; the median longitudinal fossa that is usually present in the clypeus of the worker as a rule hardly or not at all traceable in the clypeus of the male; the apico-lateral angles of the clypeus acute and almost in contact with the rim of the eye; the length of the clypeus a little more than one-half its greatest width. The labrum simple. The mandibles edentate or virtually edentate along their receding apical edge; a narrow red band immediately behind this apex, the mandibles otherwise black. The malar space almost obsolete, the inner angle of the base of the mandible very nearly in contact with the rim of the eye. The distance between the lateral ocelli distinctly greater than that which separates each lateral ocellus from the nearest compound eye. The carina behind the ocelli blunt and low to moderately developed. The head a little more hirsute than that of the worker, with short but moderately abundant black hairs on the clypeus that are somewhat comparable in length with the black hairs on the scape. The erect hairs on the front, vertex, mandibles below, and lower one-third of genal area likewise black but considerably longer than those of the clypeus and scape. Appressed silvery gray microscopic hairs over clypeus, front, and sides of face; the upper two-thirds of genal area silvery gray pruinose. The antennal sockets, a longitudinal stripe almost invariably on the

scape in front, and the flagellum below ferruginous.

THORAX: Black, of somewhat subdued sheen due to the presence of grayish tomentum, especially on the mesonotum and to an even greater extent in the area on each side of the hairless middle region of the propodeum. The erect hairs black.

LEGS: Somewhat less uniformly dark than in the workers from the same nest, with the hind tibiae and metatarsi and to some extent also the hind femora reddish brown. The hind tibiae very feebly concave along their anterior lateral contour and much more emphatically convex along their posterior lateral contour, the contour of their apex approximately round, their greatest width about four-fifths that of the conspecific worker at the corresponding level. The hind metatarsi about three-fourths as wide at their widest (near the apex) as the hind tibiae at their widest, the posterior apical extremity slightly acute to rounded. The hairs of the leg predominantly black or blackish, with the following rather inconspicuous exceptions: the tomentum on the under side of the trochanters, the dense fringe of very microscopic hairs on the under side of the femora, the short bristles at the apex of the inner face of the hind femora and the similar dense short bristles down the elevated area of the under side of the hind tibiae, as well as the appressed sericeous hairs at the base of the inner face of the hind metatarsi, whitish to silvery gray; the plumose hairs intermixed with the black simple hairs towards the posterior lateral contour of the middle tibiae and those along the posterior lateral contour of the hind tibiae somewhat duller gray to brownish; the metatarsal brushes copper colored to blackish. The mainly plumose fringe along the posterior lateral contour of the hind tibiae dense, the longer simple hairs of the fringe somewhat longer than half the maximum width of these tibiae. The distribution in general of the simple black hairs and their relative length approximately as indicated in the generalized description of the male of subgenus *Trigona*.

WINGS: Like those of the worker, smoky. Of the 181 lower wings examined, 170 had five hamuli, 10 had six hamuli, and one had four hamuli, an average of 5.05.

ABDOMEN: Black or blackish, comparable in width with the thorax. The hairs of the tergites black: tergite 1 with a narrow band apically of appressed hairs that tend to extend also upward along the sides of the tergite; tergites 2 and 3 likewise with, for the most part, appressed hairs along apex and laterally; tergites 4 to 6 with erect longer hairs; tergite 7 with a thin fringe along its apex of somewhat incurved hairs. The sericeous hairs of the venter silvery gray. For the structure of the sternites and genitalia, see figure 30.

MEASUREMENTS: Length about 5.5 mm.; width of thorax about 2.25 mm.; length of forewing, including tegula, about 6.75 to 7 mm.

TYPE MATERIAL

The type of *corvina* from Zacapa, Guatemala, December 12, 1911, was kindly donated to the American Museum of Natural History by Prof. T. D. A. Cockerell.

DISCUSSION

Cockerell (1913a, p. 12) made *corvina* a variety of *ruficrus* on the basis of the worker, but comparison of the sternites of the male, notably sternite 7, of *ruficrus* (fig. 27D) and of the corresponding parts of *corvina* (fig. 30D) makes for hesitation in considering them one, and the genitalia, too, differ slightly (figs. 27A, 30A). The dark hind tibiae can frequently be relied upon to separate the worker of *corvina* from the worker of *ruficrus*, but the fact that callow specimens of *corvina* have hind tibiae colored like those of *ruficrus* and that even *ruficrus* sometimes has abnormally darkened joints necessitates reliance on an aggregate of characters for separating the two. Of the characters listed in the description of the worker the most reliable is the limited development of the black hairs on the clypeus of *corvina*, which are usually so sparse and stunted as to be negligible. In contrast, *ruficrus* has a strong growth of erect dark hairs covering the clypeus. The median channeling of the clypeus of the worker tends to be stronger in *ruficrus* than in *corvina*. Nature has separated the two by placing *ruficrus* in South America and its near relative in Central America, where it is sometimes confused with the equally abundant *amalihea*. However, the worker of *cor-*

vina may be readily distinguished from Olivier's species by its largely red mandibles (only the teeth and basal prominences being black) and by its slightly raised and medianly channeled clypeus, in contrast to the flat clypeus of *amalihea*. The male of *corvina*, on the other hand, has, like *amalihea*, black mandibles striped at the apex with red.

In both the queens of *corvina* that I have had opportunity to examine, the second tooth of the mandible is very stunted, notably shorter than the third. Both of these specimens are from the same nest, and one would like to know (from the examination of other nests) whether this character is constant. Should this prove to be the case, it would

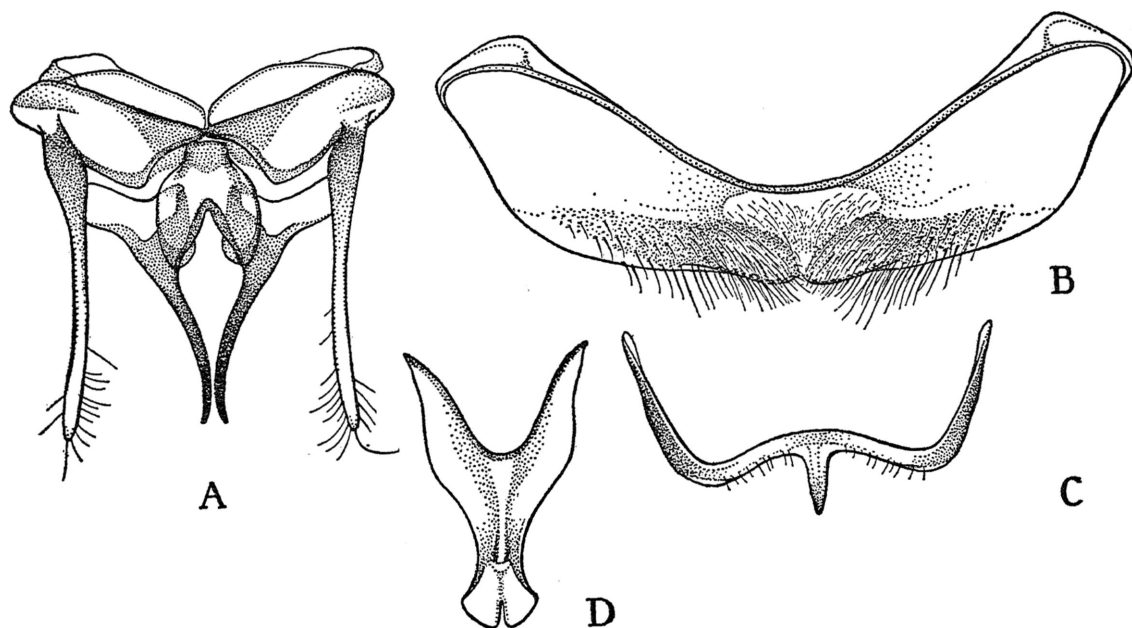


FIG. 30. Abdominal parts of the male of *Trigona* (*Trigona*) *corvina* Cockerell. A. Genitalia (chitinized parts only). B. Sternite 5. C. Sternite 6. D. Sternite 7. All based on specimens from San José, Costa Rica. Drawings by Shirley H. Risser.

The boundary line between different species of *Trigona* comes close to breaking down in the case of certain more or less aberrant specimens. Workers of *corvina* in which the median channeling of the clypeus is more than ordinarily shallow (those referred to 15 in the key to worker, p. 204) may be mistaken for *hyalinata* variety *branneri*, notwithstanding the darker wings of *corvina*. In fact, one is tempted to say that *corvina* is only a little less closely related to *hyalinata* than it is to *ruficrus*, linked by these aberrant specimens of *corvina* that approximate *hyalinata* in having a nearly unfurrowed clypeus. However, the distinctiveness of *corvina* and of *hyalinata* variety *branneri* is emphasized by a comparative study of the genitalia and particularly sternite 7 of the male (compare fig. 30A and D with fig. 20A and D).

constitute a more trustworthy means of separating the royal caste of *corvina* from that of *ruficrus* (in which the second tooth is well developed) than the coloration of the hind leg used in the key.

Because the honey and the wax of bees' nests are valued, many a *Trigona* nest is destroyed for its contents long before the natural termination of its days. Other *Trigona* communities invite destruction because of their ravages upon *Citrus* plantations. Hence it is difficult to obtain records of the normal span of life of a colony. On Barro Colorado Island, Canal Zone, several of the nests (in particular those of *Trigona fulviventris* and *Lestrimelitta limão*), which I had observed during my first visit to that research station, were still flourishing when I returned after an interval of years. For all I know they

may still be in existence. It is not to be assumed hastily that colonies of *corvina* have a greater longevity than others; probably the impressive age that some colonies of this form have attained is due to their having escaped destruction because of their location high in trees or because of some other favoring circumstance. Nevertheless, it is of interest that certain of these nests have been known to persist over long stretches of time. Thus Rau (1933, p. 36) told of "an enormous nest" of *corvina* 15 feet above the ground in a tree at New Limon, Canal Zone, that a native assured him had been there for at least six years. From F. Nevermann I obtained specimens of *corvina* from Costa Rica that were collected from what he described as "a ten-year old nest." For the most part this species seems to build rather high in the trees and to construct exposed rather than concealed nests. A very large nest of this species, weighing 69 pounds, was obtained by C. D. Michener at Juan Mina, Canal Zone, on April 27, 1945. This nest, which was located 12 feet above the ground in a grapefruit tree, was reputed to be at least 10 years old. The dimensions were 22 by 18 by 17 inches, with the long axis vertical. Michener, in a letter to me, described the nest as follows:

"Entrance in lower part of nest, about one inch in diameter, projecting slightly. Beneath the opening is a beard of small filaments 2-4 mm. in diameter and 1-3 mm. thick, brittle and easily broken, supported from within by numerous small columns. Beneath this the material of the nest is very hard and thick, so that a small axe and considerable prying were necessary to remove large pieces. This thick wax is to some extent in distinct layers, but the layers differ in number, thickness and distinctness in different parts of the nest. Where distinct and separated by open spaces, they are connected by small and large round and irregular supports, and the spaces between the layers are connected by holes through the layers. Many holes penetrate the outermost layer of heavy material to make connection with the space beneath the outer skin of brittle material.

"With this arrangement it would be difficult for an enemy to attack the nest without breaking the brittle outer coating in many places and allowing the bees to swarm out

and bite; yet because of the 2.5 to 3 inches made of layers of very strong material inside of the brittle layer, storms, falling limbs, and the like would not seriously damage the nest.

"Among the inner layers of hard material very much yellowish, solid material, apparently pollen, is stored, so that in sections some parts appear stratified or laminated. This material is firm and hard, though not strong as is the material of the hard layers, and some of it gives the appearance of having been there a long time.

"Inside of the layers of strong, hard material are groups and layers of honeypots, made of soft, dark brown wax and almost all sealed and completely full of dark honey.

"Inward of the honeypots is the brood chamber. This is a space about 14 by 9 by 9 inches, filled with about 30 horizontal combs of brood cells. The combs are irregular, so that no one completely crosses the cavity, and many have large holes in them. Thus there is ample opportunity for passage up and down among the combs. The brood cells are 3 mm. in diameter by 5 to 6 mm. in height. Here and there toward the edges of the brood chamber, where the combs are particularly irregular, is a queen cell. These are paler than the other cells, about 9 mm. long by 6.5 mm. in diameter, often irregular in shape.

"The provisions in the brood cells are a yellowish opaque liquid, in contrast to the clear dark honey in the honey pots."

A fuller description of this nest was subsequently published by Michener (1946, pp. 193-195). Michener estimated that there were 82,000 brood cells.

No physogastric queen was found. There were, however, two virgin queens. The workers and males recovered numbered 6529, which Michener calculated to be 90 per cent of the entire colony. Among the 5201 specimens sent me were 417 males and 4782 workers, or about in the proportion of one male to 11.47 workers.

None of the males from the nest just mentioned gave evidence of exuding wax. Quite a number of them had on their hind tibiae traces of sticky matter, but as such sticky matter was frequently also present in equal degree on other parts of the body (head or thorax) I am not inclined to interpret its presence on the tibiae as an evidence that these

males had been participating as artisans in the building operations of the colony. One or two even had what seemed to be pollen plastered on their face and thinly on one hind tibia, without trace, however, of any corresponding load on the other hind tibia. It seems to me most unlikely that foraging in the field accounted for this floral residue.

Be it mentioned finally that many of the workers of the nest had mites fastened to them. The favorite place for the mite to lodge was on the outer face of the hind tibiae, frequently at or towards the apex. In some instances there were mites on both hind tibiae, giving a balanced impression. In contrast, the males seemed largely free of mites, and in only a single instance was one of these creatures noted on a hind tibia.

Ferdinand Nevermann, in correspondence with me, mentioned an interesting arrangement of the cells in nests examined in Costa Rica, presumably for the most part on or near his farm (Hamburg Farm), which, he stated, is on the Reventazon River, about 15 kilometers from the Atlantic Ocean. In these nests the combs of the lower part were horizontal in position or, as he describes them, "in level plates." However, the top group of combs, in contrast, was arranged "always in spiral" and that spiral in the instances noted had a left turn.

This bee was recorded by Wheeler (1913, p. 7) busily engaged in "collecting the sticky propolis from the surfaces of young orange leaves," while Cockerell (1918d, p. 482) cited Morrison as observing *corvina* "chewing on the leaves of young *Citrus* plants." Michener (1946, p. 195) commented that: "The workers gather on the tender growing leaves and cut the margins with their mandibles. Then they apparently collect the liquid exuding from the damaged leaf margins. Such damage is sometimes so continuous as to almost prevent the growth of an orange tree."

The flowers of the banana are visited by this *Trigona* (Cockerell, 1922, p. 8, who quotes the field note of R. E. B. McKenney). Rau (1933, p. 36) noted *corvina* feeding on the fruit itself as well as gathering soft tar, especially in the early morning hours before it had become too soft. According to a field note of Wheeler, *corvina* was collected on

cashew growing at Red Tank, Canal Zone.

As are several other members of its subgenus, *corvina* is uncleanly in its habits. Wheeler (1913, p. 7) observed it at the garbage crematory at Gatun in the Canal Zone mingling in great numbers "with the houseflies and blowflies inside the empty garbage barrels where it was collecting the malodorous moisture that still clung to the wooden staves." On Barro Colorado Island I have seen *corvina* on more than one occasion frequenting the dung of *Carnivora*.

As are most of the members of the subgenus *Trigona* this species is vigorous in attack. Rau recorded (1933, p. 36) how, when he tapped on a tree where a nest of *corvina* was located, the occupants of the nest came down in swarms, clinging to his face, crawling into his nostrils and ears, and penetrating his hair and clothing, "a sticky, disgusting mass."

A name for this bee in Panama and the Canal Zone is, C. D. Michener tells me, "zegaña," but the designation is applied also to a variety of *Trigona* (*Partamona*) *testacea* that is close to *cupira*, possibly because both species construct more or less exposed arboreal nests and so are lumped together by the indiscriminating.

DISTRIBUTION

The type material of *corvina* was from the following localities: Zacapa in Guatemala, San José in Costa Rica, Gatun in the Canal Zone, and Las Sabanas in Panama. Later Cockerell (1920c, p. 465) extended the range of this form to South America on the basis of specimens from Tumatumari, British Guiana, in the American Museum collection. According to my interpretation, these specimens from Tumatumari are assignable rather to *hyalinata* variety *hyalinata*. They lack utterly the groove-like, median, longitudinal depression on the clypeus that is characteristic of typical *ruficrus* and that is present also, although sometimes only faintly, on the clypeus of *corvina*. Moreover, the wings of these Tumatumari specimens are more hyaline than is the case in *corvina*, and the black hairs on the clypeus are denser and more developed. With the rejection of the Tumatumari specimens, the known range of *corvina* is confined to Mexico and Central

America. In the collections under consideration there are specimens from the following localities:

MEXICO: Distrito Federal (J. R. Inda). State of Vera Cruz: Córdoba, June 11, 1905 (F. Knab), and 1926? (C. M. Holmes); Santa Lucrecia, June 20, 1905 (F. Knab); Coatepec (L. Conradt); Súcil, June, 1944 (M. Guerra). State of Tabasco: Teapa, March (H. H. Smith). State of Campeche: La Lucha, on Río Candelaria, about 40 meters, Jan. 11, 1939 (A. Dampf). State of Oaxaca: Upper Río Coatzacoalcas, April 23, 1945 (T. C. Schneirla).

BRITISH HONDURAS: Belize River, March 14, 1922 (H. F. Loomis); Feb. 13, 1931 (W. Morre); Sarstoon River (Blancaneau).

GUATEMALA: Río Polochic (Barber and Schwarz); Zacapa, Dec. 13, 1911 (W. M. Wheeler); Quiriguá, May 1919 (S. F. Blake); Izabal, June, 1919 (S. F. Blake); San Cristobal, Jan. (J. D. Norton); Jicaro, March 8, 1931 (D. M. Bates) and May 8, 1931 (J. Bequaert); Los Amates (Kellerman).

HONDURAS: La Ceiba, March 19, 1916, and Dec. 2, 1916 (F. J. Dyer); Choloma (W. M. Mann); Negrito, March 27, 1923 (T. H. Hubbell); Tela, on Jilamo Farm, May 25, 1923 (T. H. Hubbell); Trujillo, Sept. 3 (J. Bird); El Canal, Puerto Castilla, March 28, 1924 (J. Bequaert); Corocito, April 3, 1924 (J. Bequaert); Subirana, Department of Yoro, Dec. 12, 1932 (R. E. Stadelmann).

COSTA RICA: Pozo Azul, June, 1902 (M. A. Carriker, Jr.); Las Loras, near Puntarenas, Sept. 8, 1905 (F. Knab); Esparta, Sept. 18, 1905 (F. Knab); San José, Dec. 27, 1911 (W. M. Wheeler); Guápiles, July, 1915 (D. E. Harrower), and Nov., 1912 (W. C. Wood); Alajuela, April, 1924 (W. M. Mann); Navarro Farm, April, 1924 (H. W. Atkinson); Tres Ríos, May 3, 1924 (J. C. Bradley); Orotina, May 6-7, 1924 (J. C. Bradley); Las Conchas, 4450 feet, July 24, 1927 (Lankester and Rehn); Hamburg Farm, Aug. 28, 1936, Oct. 28, 1936, "ten-year old nest," including males, April 8, 1937, including males, April 29, 1937, May 30, 1937, Sept. 2, 1937, including males (F. Nevermann); La Caja, near San José, July 7, 1937 (F. Nevermann); San Isidro, Aug. 7, 1937 (A. Alfaro); Matina, July 15, 1937 (A. Alfaro).

PANAMA: Punta de Peña, Aug. 6, 1906, on banana flowers (R. E. B. McKenney); Old Panama, Jan. 31, 1911 (A. Busck); Cabina, May 27, 1911 (A. Busck); La Chorrera, May 17, 1912 (A. Busck); Panama City, Feb.-March, 1915; Chagres River, Oct. 9, 1917, on *Citrus* (H. Morrison); Las Sabanas, near Panama City, Nov. 17, 1923 (F. E. Lutz); Boquete, Chiriqui Province,

March 6-22, 1923 (F. M. Gage); Progreso, Chiriqui Province, April 16, 1923 (F. M. Gage); Chagres (Juan Mina); Bella Vista, April 3, 1923 (W. M. Wheeler), July 2-6, 1924 (N. Banks); Santa Rosa, Chagres River, March 13, 1933 (H. F. Schwarz); El Volcan, Chiriqui Province, Feb. 18-24, 1936 (F. E. Lutz and W. J. Gertsch).

CANAL ZONE: Paraiso, Feb. 2, 1911 (A. Busck); Gatun, Nov. 11, 1911 (W. M. Wheeler), July-Aug. 1915 (D. E. Harrower); Ancon (J. Zetek), Jan. 14-16, 1914 (T. Hallinan); Corozal, Feb. 23, 1914, (T. Hallinan); Balboa, June 28, 1914, and Nov. 18, 1914 (T. Hallinan), and Nov. 19, 1930 (H. F. Schwarz); Culebra, Sept. 27, 1914, and Nov. 22, 1914 (T. Hallinan); Quebrada de Oro, March 13, 1923 (W. M. Wheeler); Red Tank, April 10, 1923, on cashew (W. M. Wheeler); Barro Colorado Island, Nov. 9-12, 1923 (F. E. Lutz), Nov. 12, 1923 (Sotero Murillo), March 25-26, 1924, and April 1-10, 1924 (J. C. Bradley), July 12-17, 1924 (N. Banks), Jan. 11, 1929 (C. H. Curran), Nov. 14, 1930, and Dec. 1, 1930, on dung of *Carnivora* near rear lighthouse (H. F. Schwarz), Feb. 27, 1933, March 2, 1933, March 5, 1933 (F. E. Lutz), March 4-6, 1933 (H. F. Schwarz); Punta Patilla, June 15, 1929 (C. H. Curran); Summit, Nov. 26, 1930 (H. F. Schwarz); Juan Mina, April 27, 1945, two virgin queens, males, and workers (C. D. Michener).

Trigona (Trigona) nigerrima Cresson

Trigona nigerrima CRESSON, 1878, p. 181.

Melipona nigerrima, DALLA TORRE, 1896, p. 581.

? *Trigona nigerrima*, COCKERELL, 1912d, p. 492.

Trigona nigerrima, CRESSON, 1916, p. 125.

? *Trigona nigerrima*, FRIESE, 1917, pp. 288, 299.

Trigona nigerrima, SCHWARZ, 1934, pp. 3, 10-11.

WORKER

DIAGNOSTIC CHARACTERS: Black. Mandible five toothed, basally often more extensively black than is usual in species of mainly reddish mandible. Length of malar space about equal to width of flagellum. Width of clypeus, at its widest, three times as great as its length. Clypeus gently arched, foveate at its apical middle, sometimes with a faint incised line bisecting it longitudinally. Black erect hairs on clypeus, supraclypeus, and scape. Posterior contour of scutellum semi-circular. Hind tibiae notably wide, exceptional in being truncate or nearly truncate along the apex and hence without the usual apical angle posteriorly. Wings rather strongly darkened.

HEAD (FIG. 21F): Black or mainly black. The facial quadrangle wide, the distance between the compound eyes at the level just below the anterior ocellus barely greater than the distance between the anterior ocellus and the apex of the clypeus. The compound eyes somewhat convergent below, the distance that separates them at their level of greatest approximation (below) being about as 7.75 is to 8.75 when compared with their divergence at the level just below the anterior ocellus. The clypeus gently arched, rising only a little above the sides of the face, foveate at the middle of the apex, and in some specimens, in addition, with a very faint bisecting longitudinal incised line traceable in certain lights from the base to nearly the apex of the clypeus (this is the case in the type specimen); the width of the clypeus, measured from one apico-lateral extremity to the other, is three times its length; the apico-lateral extremities separated from the compound eye by about the width of the flagellum. The supraclypeus fairly prominent. The labrum simple. The mandibles (fig. 31) armed with five teeth, the inner four of which usually tend to be relatively shorter and blunter than is the case in most of the other five-toothed species of the subgenus *Trigona* with the exception of *dimidiata* Smith and its variety *venezuelana*. The malar space at its middle about as long as the flagellum is wide. The distance between the lateral ocelli somewhat less than that which separates each lateral ocellus from the nearest compound eye. The carina behind the ocelli moderately developed and somewhat blunt. Clypeus, front, vertex, and lower one-third of genal area more or less moderately shiny. The clypeus and front a little less densely covered with silvery gray appressed microscopic hairs than are the sides of the face; the upper two-thirds of the genal area silvery gray pruinose (in some lights now and then even a little olivaceous towards its upper extremity). The longer, erect, and coarser hairs of the head black, present on the clypeus, supraclypeus, front, vertex, lower one-third of genal area, and fringing the lower edge of the black basal part of the mandibles, while the more or less extensively brownish or reddish apical part of the mandibles is fringed below usually with copper-colored or reddish

hairs. There are a very few short, erect, black hairs also usually interspersed among the appressed silvery gray hairs of the sides of the face and genal area. The erect black hairs on the clypeus, especially on the apical half of the clypeus, rather notably longer

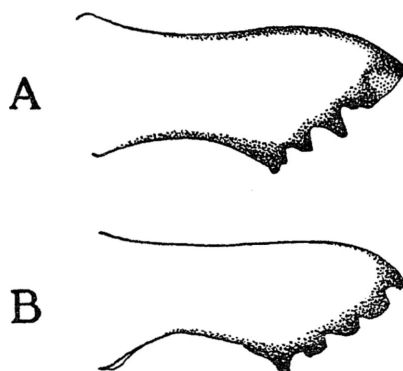


FIG. 31. Mandible of workers of *Trigona* (*Trigona*) *nigerrima* Cresson. Sometimes a thin septum of chitin (A) is found connecting teeth that ordinarily are separated. With the manipulation of resinous or other substances this septum is doubtless often chipped off, and the teeth of the mandible tend to wear down. B. Another specimen from the same locality and part of a large series with identical data, suggesting that all the specimens may have been collected from the same nest, shows what is probably a wearing down of the teeth through use rather than an initial difference of structure, although individual differences sometimes occur from specimen to specimen not only in this species but in others. The tiny emargination on the innermost tooth of specimen A is to be regarded as such an aberration. The mandibles are inverted in the figure.

than the somewhat coarse hairs of the scape and not much shorter than the hairs towards the middle or even upper part of the front. The clypeus usually black as is the rest of the head but in some cases dark reddish black; the supraclypeus, on the other hand, is almost invariably an undiluted black even when, in callows, the clypeus is wholly or predominantly tawny. The labrum reddish to blackish. The basal part of the mandible (usually considerably more than the basal prominences and sometimes more than the basal half) black or blackish; the apical part (except for the black apical teeth) more or less reddish or brownish. The antennal sock-

ets ferruginous; the scape usually wholly black; the flagellum sometimes ferruginous to more or less dull brown beneath but in other cases little differentiated from the dark upper surface.

THORAX: Black, of rather subdued sheen due to the presence of grayish tomentum on mesonotum, scutellum, pleura, and especially sides of propodeum in addition to the longer, more conspicuous but sparser simple black

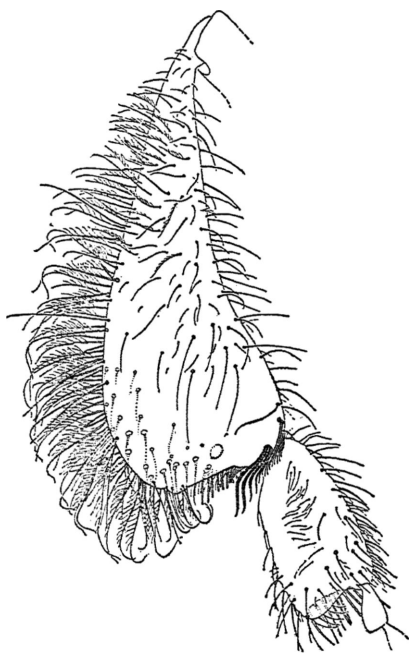


FIG. 32. Hind tibia and metatarsus of worker of *Trigona (Trigona) nigerrima* Cresson. Drawing by Alice Gray.

hairs in these areas. The relative length of the hairs as indicated in the description of the subgenus *Trigona*. The scutellum not in the least protuberant posteriorly, its hind contour semicircular.

LEGS: Prevailing black or blackish, even the tarsal joints with the exception of the apical segment usually more inclined to black than to ferruginous, but in callow specimens the legs may be largely or wholly light brown. The hind tibiae (fig. 32) notably wide, clavate in outline, much wider at the apex than at the base, their anterior lateral contour somewhat concave, their posterior

lateral contour emphatically convex, their apical contour exceptional in being truncate or virtually truncate so that the angle, usual in so many species of the subgenus *Trigona*, where the apical contour and the posterior contour meet, is wanting, and the point of attachment anteriorly for compound comb is barely differentiated from the rest of the apical contour. The outer face of the hind tibiae very gently arched over approximately its basal two-thirds, flattened (especially posteriorly) on approximately its apical one-third. The flattened area constituting the posterior part of the under side of the hind tibiae about two-fifths the width of the joint towards the apex. The hind metatarsi rather parallel sided, about three-fifths as wide as the greatest width of the associated tibiae, their posterior apical angle slightly acute to almost rectangular. The hairs of the legs predominantly black but with the following relatively minor exceptions: the plumose hairs intermixed with the black simple hairs on the external face of the middle tibiae and extending usually to the basal and posterior part of the corresponding metatarsi as well as the similar hairs along the posterior contour of the hind tibiae grayish brown; the microscopic but stubby hairs on the elevated part of the under side of the hind tibiae and adjacent apical part beneath of the hind femora silvery gray; the suboval sericeous patch at the base of the under side of the hind metatarsi silvery gray to whitish, although sometimes the surface is covered with a sticky substance that tends to conceal the true coloration; the metatarsal brushes are copper colored to golden. The relative length of the hairs and their distribution as indicated in the description of the worker of the subgenus *Trigona*.

WINGS: Rather strongly darkened, the stain rather comparable in intensity with that of *trinidensis*; the median cell somewhat darker than the other cells, and the apical part of the wing a little lighter than the basal. The transverse cubital veins as a rule fairly clearly indicated. First discoidal cell about three-fourths as long as the marginal cell. Number of hamuli on each hind wing usually six, rarely five or seven. Of 124 wings examined, 114 had six hamuli, five had five hamuli, and five had seven hamuli, an

average of six hamuli. The tegulae black or blackish.

ABDOMEN: Black or blackish, more often with the median and apical tergites at least partly exposed rather than telescoped, trigonate, with a width that approximates that of the thorax. Tergite 2 with a narrow apical band of dense, appressed, dark, microscopic hairs; tergite 3 with a little fuller band of similar hairs and, in addition, semi-erect blackish hairs, the hirsute area faintly tessellated; the subsequent tergites with erect black hairs covering their exposed or most of their exposed surface and slightly granular where these hairs emerge, but otherwise smooth. Approximately the apical half of the several sternites with erect black hairs at the middle, these hairs grading into sericeous patches at each side. When the abdomen is telescoped, the hair bands form a continuously hairy surface. The tomentum on sternite 6 sometimes pale rather than black and the erect hairs few on this sternite.

MEASUREMENTS: Length 6 to 7 mm.; width of thorax 2.25 to 2.5 mm.; length of forewing, including tegula, 8 to 8.5 mm.

QUEEN (VIRGIN)¹

HEAD (FIG. 21E): A trifle wider than the mesonotum but narrower than the distance from the outer rim of one of the tegulae to the outer rim of the other. The facial quadrangle wide, the distance between the compound eyes at the level just below the anterior ocellus about equal to the distance separating the anterior ocellus from the apical margin of the clypeus. The eyes almost parallel to each other, barely convergent below, a little shorter than those of the worker (in the proportion of about 4.5 to 5) and distinctly narrower. The eyes without hairs. The clypeus gently arched but, unlike that of the worker, not foveate at the middle of the apex. The width of the clypeus, measured from one apico-lateral extremity to the other, about twice its length. The supraclypeus, like the clypeus, raised somewhat above the sides of the face. The labrum simple, its apical contour gently rounded. The dentition along the apical margin of the mandible indistinct, the two innermost of the five teeth traced only

with difficulty. The malar space distinctly longer than the scape (exclusive of its hairs) is wide. The ocelli small and remote from the compound eyes; the distance separating the lateral ocelli from each other is about one-half that between each lateral ocellus and the nearest compound eye. The carina behind the ocelli moderately developed and blunt. More or less shiny are all parts of the face, but genal area is clothed densely over approximately its upper two-thirds with silvery gray to yellowish, microscopic, sericeous hairs, which also reveal themselves as being rather dense over the front and the sides of the face when the insect is viewed from above. Far more conspicuous, however, is the heavy bearding of coarse, long, grayish to stramineous hairs that covers especially the lower half of the face, the hairs over the outer face of the mandibles and particularly those along the inferior edge of the mandibles and bristling from the clypeus, supraclypeus, and labrum being in many cases notably longer than the mandible is wide at the base. The outer face of the scape with a similar thick covering of coarse hairs, the length of which in some cases approximates twice the width of the scape. The long hairs on the front more sparse except towards the upper reaches, but even the relatively long grayish hairs of the vertex shorter and less conspicuous than those of, for instance, the clypeus, and the fairly long gray hairs of the lower one-third of genal area also distinctly shorter than the clypeal hairs. The chitin predominantly fuscous to black. The mandibles black basally but reddish over their apical one-half except for the slightly darkened apical edge. The clypeus more or less reddish brown. The scape dark but the flagellum (if one may judge from the condition of the basal joints, the only ones that have survived in the specimens before me) dark above but ferruginous below.

THORAX: Black to here and there brownish, wider than that of the worker. The length of the mesonotum plus scutellum about equal to the width of the mesonotum at the base. Dark appressed hairs over the mesonotum and pleura and, in addition, erect, rather long (comparable to those on the clypeus), yellowish to fuscous hairs on the mesonotum and mesopleura, and still longer hairs on the

¹ Description based on two specimens from Middlesex, British Honduras.

scutellum. The middle area of the propodeum hairless and shiny.

LEGS: Reddish brown to blackish, with the femora a little more uniformly dark than the tibiae. The hind tibiae about the same length as the hind femora plus the hind trochanters, somewhat clavate in outline, widely angular anteriorly at the apex, rather rounded posteriorly at the apex. The hind metatarsi about two-thirds the width of the hind tibiae at the apex, and slightly tapering from near the base to the apex; the combined small joints of the hind tarsi about as long as the metatarsi measured along their inner face; the fine light golden bristles nearly as dense at the base as they are at the apex of the inner face of the joint. Similar fine bristles are present on the inner face of the metatarsi of the fore and middle legs. The other hairs of the legs grayish to slightly fuscous (especially on the hind tibiae) and on the whole long and coarse, particularly so on the outer face of all the tibiae and the posterior lateral margin of the tarsi, particularly of the metatarsi. The hairs on the outer face of the tibiae progressively longer from fore pair to hind pair; the hairs of the outer face of the middle tibiae simple, being without traceable admixture of plumose hairs; the hairs along the posterior lateral contour of the hind tibiae exceedingly long, for the most part not shorter (in some cases longer) than the greatest width of the hind metatarsus. The hairs paler, finer, shorter, and very dense on the under side of the trochanters and femora, and relatively short hairs also on the outer (anterior) face of the femora in contrast to the more glabrous condition of the inner (posterior) face.

WINGS: Smoky, of somewhat deeper tinge in the median cell, a little longer than those of the worker. Tegulae fuscous. Number of hamuli, in the only two wings available for examination, respectively six and seven.

ABDOMEN: Blackish to brownish. Tergite 1 glabrous or virtually glabrous; tergite 2 with very microscopic appressed gray hairs thinly scattered over its surface; tergite 3 likewise with microscopic appressed gray hairs but these very dense throughout; tergites 4 and 5 with similar but slightly longer gray appressed hairs and, in addition, with moderately long, erect, fine gray hairs; tergite 6 with still longer erect gray hairs in

addition to the concolorous appressed hairs. Where the hairs emerge, the surface appears more or less finely punctate. The erect hairs along the apex of the several sternites gray.

MEASUREMENTS: Length about 7.5 mm.; width of thorax about 2.75 mm.; length of forewing, including tegula, about 8.5 mm.

MALE

HEAD (FIG. 21G): Black. The facial quadrangle not so wide as that of the worker. The distance from one eye to the other at their level of closest approximation (below) somewhat less than three-quarters of the length of the eye, whereas in the worker the eye is subequal in length to the distance separating one eye from the other at their level of maximum convergence. The clypeus and supraclypeus rising somewhat above the level of the sides of the face; the clypeus of rather even surface, not (as is that of the worker) foveate at its apical middle or with a faintly incised longitudinal bisection, the apicolateral extremities acute and separated from the eye by an interval distinctly less than the width of the tapering flagellum at its apex, the length of the clypeus about one-half its greatest width. The labrum simple. The mandibles virtually smooth along their inwardly receding apical edge, devoid of dentition; a red stripe traverses the mandible behind the apical edge. The malar space fairly distinct even though short, not wholly obsolete. The distance between the lateral ocelli barely greater than the distance separating each lateral ocellus from the nearest compound eye. The carina behind the ocelli moderately developed and rather blunt. The head with longer erect black hairs than is the case in the worker. The clypeus especially with much longer and more abundant black hairs, those of the lower half of the clypeus tending to exceed in length the black hairs of the scape, which in turn are subequal to the width of the scape. The supraclypeus, in contrast, almost glabrous, with only a few stunted hairs. The chitin of the clypeus slightly tessellated, especially where the hairs are concentrated. Longish black hairs on the front, especially the upper part, on the vertex, labrum, inferior margin of clypeus, and lower one-third of genal area. There are short black hairs among the silvery

gray appressed hairs on the sides of the face. The appressed silvery gray hairs extend also over the clypeus and are particularly dense on the upper two-thirds of the genal area. The antennal sockets, a stripe in front on the otherwise black scape, and the under side of the flagellum ferruginous.

THORAX: Black, about as shiny as the upper part of the head although covered with rather dull grayish tomentum to the inclusion

hind metatarsi towards the apex about three-fifths as wide as the hind tibiae and a little thicker anteriorly (particularly on the basal one-half) than posteriorly; the posterior apical extremity of the hind metatarsi subrectangular to slightly rounded. The hairs of the legs predominantly black to blackish, with the following rather minor exceptions: the tomentum of the under side of the trochanters (or at least as a rule that

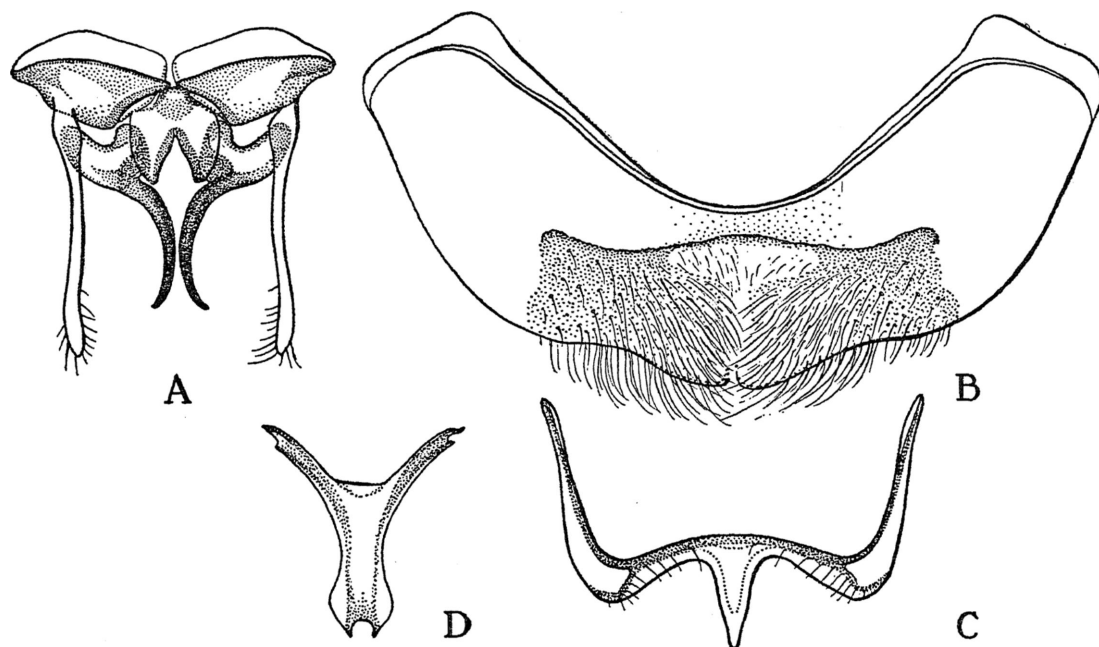


FIG. 33. Abdominal parts of male of *Trigona* (*Trigona*) *nigerrima* Cresson. A. Genitalia (chitinized parts only). B. Sternite 5. C. Sternite 6. D. Sternite 7. All based on a specimen from Balboa, Canal Zone. Drawings by Shirley H. Risser.

of the area on each side of the bare middle region of the propodeum. The erect hairs of the thorax and propodeum black.

LEGS: Black, but with invasions or replacements of brown, more particularly on the hind tibiae and hind metatarsi. The hind tibiae feebly concave along their anterior lateral contour and much more emphatically convex along their posterior lateral contour; the contour of the apex of these tibiae approximating the round, only briefly and not nearly so distinctly truncate as is the case in the worker; the outer face of these tibiae flattened towards the apex posteriorly; their greatest width (near the apex) about six-sevenths that of the conspecific worker. The

of the first pair) rather dull grayish; the very microscopic fringes (often difficult to detect) on the under side of the femora somewhat grayish; the short bristles at the apex of the inner face of the hind femora and the similar dense short bristles down the elevated area of the under side of the hind tibiae as well as the sericeous flattened hairs at the base of the under side of hind metatarsi silvery gray; the more erect hairs on the apical two-thirds of the under side of the hind metatarsi copper colored to blackish, as are likewise the metatarsal brushes on the fore and middle legs. The fringe along the posterior lateral margin of the hind tibiae with abundant plumose hairs (such hairs also plentiful on the outer

face of the middle tibiae), the longer interspersed simple hairs of this fringe at least two-thirds the maximum width of the joint. The distribution of the simple black hairs in general and their relative length approximately as indicated in the generalized description of the male of subgenus *Trigona*.

WINGS: As in the worker, rather strongly smoky. Number of hamuli per lower wing, in the nine wings examined, was six in eight of the cases and five in the ninth case, an average of 5.88.

ABDOMEN: Black. Approximating the thorax in width. The hairs of the tergites black: those of tergites 2 and 3 appressed, forming a narrow band along the apex; those on tergites 4 to 6 longer and erect; tergite 7 with a thin fringe of incurved hairs. The sericeous hairs of the venter rather dull gray. For the structure of the sternites and genitalia, see figure 33.

MEASUREMENTS: Length 6.5 to 7 mm.; width of thorax about 2.5 mm.; length of forewing, including tegula, about 8 mm.

TYPE MATERIAL

The holotype from Mexico is in the Academy of Natural Sciences of Philadelphia.

DISCUSSION

This species is apt to be confused with *Trigona* (*Trigona*) *trinidadiansis* Provancher and particularly with its variety *silvestriana*, which has somewhat the same range. Yet there are certain well-marked structural differences which, singly or in combination, can be relied upon to separate the two groups of insects. In the hind tibiae of the worker of *silvestriana* the angle near the posterior end of the apex is sharp owing to the emargination of the apical edge of the joint; in the worker of *nigerrima*, on the other hand, the apical edge is truncate and the posterior apical contour is in consequence uninterruptedly rounded and angleless or barely angulate inward of the posterior curvature (a few specimens from the Canal Zone). The scutellum taken in conjunction with the axillae tends in *trinidadiansis* and its variety *silvestriana* to be somewhat elongately curved to very bluntly pointed, while in *nigerrima* it is uniformly semicircular. Finally there is a difference in the relationship of the antennal joints; joint 3 in the worker of *trinidadiansis*

and its variety *silvestriana* is longer than broad and subequal to joint 4, whereas in the worker of *nigerrima* joint 3 viewed from beneath is very short, being distinctly broader than long, and emphatically shorter than joint 4. To these plastic characters certain more superficial characters may be added: the mandibles of the worker of *trinidadiansis* and its variety *silvestriana* are usually mostly red or brown, a basal black area other than the prominences being rare; in mature specimens of the worker of *nigerrima*, on the other hand, the base of the mandibles and the teeth are habitually black, although there is an extensive reddish or brownish area on the apical half (broader than is the corresponding area in *amalihea*). *Trigona nigerrima*, like typical *trinidadiansis* and unlike *trinidadiansis* variety *silvestriana*, has black hairs on the clypeus, coarse, black hairs on the front, and short, coarse hairs on the scape. In size it is somewhat smaller and daintier than even the smaller individuals of *trinidadiansis* variety *silvestriana*.

Certain collectors (H. B. Smart, A. Busck, E. J. Hambleton) have reported *nigerrima* on *Citrus*; Bequaert took it on the flowers of *Sclerocarpus divaricatus*.

According to a report received from Dr. B. A. Krukoff of the New York Botanical Garden, *nigerrima* caused damage in Guatemala to flowers of *Crotalaria agathiflora*. Such was the destruction wrought by the bees that after their devastations it was impossible to obtain the regular supply of seeds required for new plantations. *Crotalaria agathiflora*, Dr. Krukoff informed me, is an African plant and was introduced into Guatemala as a cover crop for *Cinchona*. The ravages that he reported occurred at Finca Naranjo of Experimental Plantations, Inc., Department of Suchitepequez, at an elevation of 3000 to 5000 feet. From Dr. C. F. W. Muesebeck I have also received specimens of *nigerrima* taken in Guatemala on *Crotalaria*. Dr. Muesebeck commented: "The form occurring on *Crotalaria* is said to gnaw through the flowers, cutting off the pistils, with the result that no fruit is produced."

DISTRIBUTION

From Mexico (type) to Panama and isolated instances in western South America.

A record was reported by Cockerell (1912d, p. 492) from Peru, and I have seen what is undoubtedly *nigerrima* from Colombia. The specimens in the collection before me are from the following localities:

MEXICO: State of Vera Cruz: Córdoba, Dec. 17, 1907 (F. Knab). State of Guerrero: Ayotzinapa, Tixtla Valley, 1600 meters, Jan. 20, 1941 (A. Dampf). State of Oaxaca: Loma Tuxtepec, April 29, 1945 (T. C. Schneirla).

BRITISH HONDURAS: Middlesex, April 10, 1931, workers, males, queens (H. B. Smart) *ex Citrus*.

GUATEMALA: Department of Santa Rosa: Chiquimulilla, 300 meters, March, 1923 (René Lichy). Department of Guatemala: Guatemala City, 5000 feet (Champion). Department of Alta Vera Paz: Cacao, Trece Aguas, Nov., 1905 (G. P. Goll). Department of Retalhuleu: San Sebastián, 1925 (L. Thiel), and June 14, 1931 (D. M. Bates). Mocá, 1000 meters, at flowers of *Sclerocarpus divaricatus*,¹ March–April, 1931 (J. Bequaert), May 2, 1921 (D. M. Bates), and March 22, 1935 (W. M. Wheeler). Department of Suchitepequez: Finca Naranjo of Experimental Plantations, Inc., 3000 to 5000 feet, on *Crotalaria agathiflora*. Tiquisata [Tiquizate?], June 21, 1945, on *Citrus* (E. J. Hambleton).

COSTA RICA: Hamburg Farm, Aug. 20, 1936 (F. Nevermann); San José, July 15, 1937 (A. Alfaro); Cache (H. R. Rogers).

HONDURAS: Monte Cristo (W. M. Mann); Cecilia (W. M. Mann); Portillo Grande, Sept. 3 (R. E. Stadelmann).

CANAL ZONE: Balboa, May 23, 1914, male (T. Hallinan); Frijoles, July 10, 1924 (N. Banks); Barro Colorado Island, July 30, 1924, and Aug. 2, 1924 (N. Banks); Dec. 21–30, 1928 (C. H. Curran), Nov. 8, 1930 (E. I. Huntington, on Wheeler Trail), Nov. 11, 1930 (H. F. Schwarz, on Drayton Trail); Tabernilla, July 20, 1907 (August Busck).

PANAMA: Bugaba, 800 to 1500 feet (Champion); Río Trinidad, May 7, 1911, on *Citrus* (August Busck); El Volcan, Chiriquí, Feb. 18, 1936 (W. J. Gertsch), Feb. 25, 1936, and Feb. 27, 1936 (F. E. Lutz).

COLOMBIA: Department of Santander: Boca del Rosario, 1936 (J. Bequaert); Puerto Olaya, 100 meters, 1936, male (J. Bequaert).

***Trigona (Trigona) dimidiata* variety
dimidiata F. Smith**

Trigona dimidiata F. SMITH, 1854, p. 411.

Melipona dimidiata, DALLA TORRE, 1896, p. 577.

¹ The plant was identified by Mr. Standley from specimens collected by Dr. Bequaert.

Trigona atroalba DUCKE, 1908a, p. 35.

Trigona dimidiata, MARIANNO, 1911, p. 91.

Melipona dimidiata, DUCKE, 1916, p. 14, opposite p. 28, pp. 74–75.

Melipona dimidiata, DUCKE, 1925, pp. 343, 351, 386.

Trigona dimidiata, MOURE, 1944a, p. 73.

Melipona dimidiata, DUCKE, 1945, pp. 1–3, opposite p. 24, pp. 58–59.

WORKER

DIAGNOSTIC CHARACTERS: Black. Mandible five toothed, the inner four shorter and blunter than in most species of subgenus *Trigona*; mandible usually reddish in large part. Length of malar space comparable to the width of the flagellum. Clypeus at its widest three times as wide as long, more or less strongly foveate at the middle of its apex, sometimes with a hair-fine shiny line medianly from base to apex. Erect black hairs on clypeus and scape but lower half of supraclypeus bare. Hind contour of scutellum semicircular. Hind tibiae usually with an inwardly placed angle posteriorly at the apex, but the apical contour in rare cases almost truncate. This species is especially distinguished by the contrast between the brown basal half of the wing and the milky apical half.

HEAD: Black or predominantly black. The facial quadrangle wide, the distance between the compound eyes at the level just below the anterior ocellus about in the proportion of 11 to 10 when compared with the distance from the middle ocellus to the apex of the clypeus. The compound eyes somewhat convergent below, the distance that separates them at their level of greatest approximation (below) being about as 9.5 is to 11 when compared to their divergence at the level just below the middle ocellus. The clypeus raised a little above the level of the adjacent sides of the face, more or less strongly foveate at the middle of its apex, and sometimes with a narrow shiny line from base to apex down its middle. The clypeus short and wide, the distance from one of its apico-lateral extremities to the other being three times as great as its length; these apico-lateral extremities separated each from the nearest compound eye by less than the width of the flagellum. The supraclypeus more prominent than the clypeus, swollen when viewed in profile. The

labrum simple. The mandibles (fig. 34) armed with five teeth; these teeth, with the exception of the outermost, tend to be rather shorter and blunter in relation to the size of the insect than is the case in most other bees of the subgenus *Trigona*. The malar space measured from the lower extremity of the eye to the base of the mandible at the

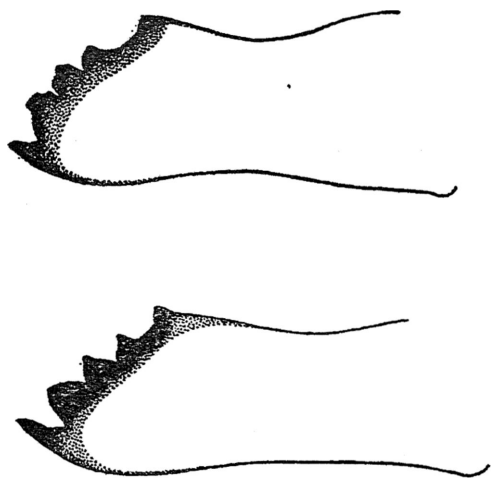


FIG. 34. Mandible of workers of *Trigona* (*Trigona*) *dimidiata* F. Smith. Individual differences, either inherent or due to wear, occur now and then in the dentition, as evidenced by these two specimens. Drawings by Alice Gray.

middle somewhat comparable in length to the width of the flagellum. The distance between the lateral ocelli about two-thirds that which separates each lateral ocellus from the nearest compound eye. A blunt and thick carina behind the ocelli. Clypeus, front, vertex, and lower one-third of genal area more or less moderately shiny, although silvery gray appressed hairs are present on all of these parts, being pruinose on the upper two-thirds of the genal area and of only slightly less density on the sides of the face, the pruinosity of the genal area in some lights dull yellowish brown to olivaceous, but in other lights silvery gray. The erect hairs of the head black with the exception of those fringing the mandible below, which, barring usually those at the very base, are reddish to copper colored. The hairs on the clypeus are relatively long (particularly those on the lower half of the clypeus and its apico-lateral extensions) and

somewhat comparable in length to, or longer than, the hairs of the scape, although shorter than those towards the upper part of the front and still shorter than those on the vertex, lower one-third of genal area, and mandibles below. The lower one-half of the supra-clypeus is bare and shiny in contrast with the upper one-half, which has a few coarse, rather long, black bristles. Predominantly black, *dimidiata* is frequently more or less reddish brown on the clypeus and genal area, sometimes on the labrum, almost invariably so over the mandibles except for the black apical teeth and the often somewhat dark-

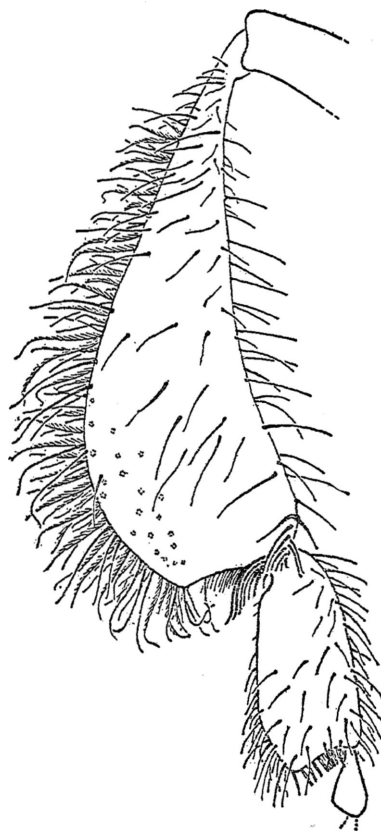


FIG. 35. Hind tibia and metatarsus of worker of *Trigona* (*Trigona*) *dimidiata* F. Smith. Drawing by Alice Gray.

ened base,¹ and now and then with a brownish stripe along the scape in front; in other cases the scape is wholly black, whereas the flagel-

¹ A series from Satipo, Peru, is exceptional in having the mandibles largely black.

lum is usually at least cloudy reddish on the under side.

THORAX: Dark, black or blackish on the mesonotum, sometimes more rufo-piceous to brownish on the pleura and propodeum, of subdued sheen due to the presence of grayish tomentum on the mesonotum, scutellum, pleura, and sides of propodeum in addition to the longer, more conspicuous but sparser simple black hairs in these areas. The relative length of the hairs as indicated in the description of the subgenus *Trigona*. The scutellum not in the least protuberant posteriorly, its hind contour semicircular.

at the apex posteriorly. The hairs of the legs predominantly black with the following relatively minor exceptions: the plumose hairs intermixed with the black simple hairs on the external face of the middle tibiae and extending usually to the basal and posterior part of the corresponding metatarsi as well as the similar hairs fringing the posterior contour of the hind tibiae dark grayish to brownish; the microscopic but stubby hairs on the elevated part of the under side of the hind tibiae and adjacent apical part beneath of the hind femora silvery gray; the suboval sericeous patch at the base of the under side of the hind

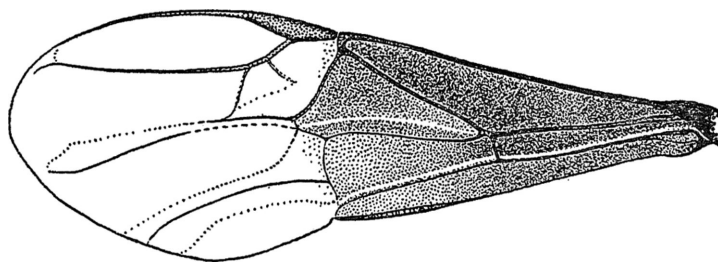


FIG. 36. Forewing of *Trigona (Trigona) dimidiata* F. Smith.
Drawing by Alice Gray.

LEGS: Dark, deep brownish to blackish. The hind tibiae (fig. 35) wide, clavate in outline, much wider at the apex than at the base; their anterior lateral contour faintly concave; their posterior lateral contour emphatically convex; their apex with an inconspicuous angle anteriorly that bears the multi-toothed tibial comb; beyond the comb the apical contour is in the main shallowly emarginate (sometimes this emargination is so shallow that it degenerates into a truncation, but usually an inwardly placed angle is clearly discernible where the apical contour and the posterior contour meet). The outer face of the hind tibiae mildly arched anteriorly and basally, flattened posteriorly and apically, and at the apical extremity very slightly concave. The flattened area constituting the posterior part of the under side of the hind tibiae about two-fifths of the width of the joint towards the apex. The hind metatarsi about three-fifths as wide at their widest as the hind tibiae, their posterior contour slightly convex, with a blunt angle

metatarsi silvery gray to whitish, but its coloration often disguised by adherent sticky matter; the metatarsal brushes black to copper colored, depending somewhat on the angle from which they are viewed. The relative length of the hairs and their distribution as indicated in the description of the worker of the subgenus *Trigona*.

WINGS (FIG. 36): Very long and sharply contrasted, the basal one-half of the wing being of iodine stain and with dark venation, the apical one-half milky white with bright ferruginous venation to the inclusion of the stigma. The marginal vein with a tendency to fade out at its apical extremity. The transverse cubital veins very faintly indicated to absent. The first discoidal cell about three-fourths as long as the marginal cell. The number of hamuli per lower wing ranges from five to seven. Only one of the 72 wings examined had as few as five hamuli, and only nine as many as seven, whereas 62 had six hamuli, an average of 6.11 hamuli. The tegulae fuscous.

ABDOMEN: Usually elongate, with the segments tending to be exposed, trigonate, somewhat narrower than the thorax, brownish black to black, the tergites of the apical half of the abdomen usually a little darker than those basally located. Tergite 2 with a narrow apical band of dense, appressed, dark, microscopic hairs; tergite 3 with a slightly fuller band of similar hairs and in addition with a few erect hairs, the hirsute area on both tergites 2 and 3 tending to be faintly tessellated; the subsequent tergites with erect black hairs covering their exposed or most of their exposed surface and slightly granular where these hairs emerge, although otherwise smooth. Approximately the apical one-half of the sternites with erect black hairs at the middle, these hairs grading into sericeous patches on each side. The tomentum of sternite 6 is sometimes golden rather than black, and the erect hairs on this sternite are relatively few.

MEASUREMENTS: Length 7.5 (abdomen more or less telescoped) to 10 mm.; width of thorax about 3 mm.; length of forewing, including tegula, about 10.5 to 10.75 mm.

QUEEN

Unknown.

MALE

Unknown.

TYPE MATERIAL

This insect does not seem to be represented among the *Trigona* described by F. Smith that were deposited in the British Museum (Natural History). In the "Catalogue of hymenopterous insects in the collection of the British Museum" (F. Smith, 1854, p. 411) the phrase "Coll. F. Smith" appears after the description of *T. dimidiata*, and this phrase does not appear after any other *Trigona* mentioned or described in that catalogue. It is possible that Smith's description was based on a unique specimen of this relatively rare insect and that this specimen (from Brazil) is the one in the Smith collection at Oxford University. Smith in his description recorded the insect as coming from Pará.

DISCUSSION

Trigona dimidiata and its variety *venezuelana* are easily differentiated from most Neotropical *Trigona* by the sharply con-

trasted coloration of the basal half and the apical half of the wings. In this respect they much more nearly resemble such Indo-Malayan species as *apicalis* F. Smith and its varieties and some of the varieties of *atripes* F. Smith than they do such New World forms as *compressa* Latreille and *tataira* variety *obscura* Friese, which also tend to have some of the cells of the wing contrasted.

Frederick Smith (1854, p. 411) gives the length of *dimidiata* as 4.5 lines, which would indicate that he had before him the larger of the two varieties of this insect.

Comparatively few records are available that throw light on the biology of *dimidiata*. Regarding the nest there is the following, communicated to me by Dr. W. Weyrauch, who came upon a colony at Satipo, near Huancayo, Peru: "Nest on trunk of tree. Inner envelope of wax, outer envelope of vegetable material. Inner envelope consisting of six layers, outer envelope of five layers. Nest measured on the outside 26 cm. wide by 30 cm. in length. Brood-chamber with combs was 11 cm. wide and 12 cm. high. Cells 9 mm. long. Four combs; honey pots."

Ducke (1908a, p. 35) recorded noting this species only on certain very humid mornings, on the trunks of old trees of the forest, and in a later account (1925, p. 386) affirmed that the bees flew only in the early morning when the air is heavy with moisture.

DISTRIBUTION

Frederick Smith (1854, p. 411) described *dimidiata* from Pará, Brazil, but Ducke never came upon the species in that locality (1916, p. 75; 1925, p. 386; 1945, p. 59). Ducke's summary of the distribution of *dimidiata* is, "Upper Amazon region including the northwestern part of Matto Grosso, and the tropical Andes." He included in the range localities in Colombia, Peru, and the Brazilian States of Amazonas and Matto Grosso. The specimens before me were collected in the following regions:

ECUADOR: Sucua, Río Upano, Feb. 3, 1939 (H. Bassler).

PERU: Río Tapiche, Dec. 14, 1923 (H. Bassler); Moyobamba region, July 5, 1925 (H. Bassler); Satipo, near Huancayo, 600 meters, Aug. 1, 1940, No. 117 (W. Weyrauch).

BOLIVIA: Tarata, 1900; Mapiri, 1900; La Paz.

BRAZIL: State of Amazonas: Santo Antonio do Iça. State of Matto Grosso: Corumbá.

Trigona (Trigona) dimidiata variety
venezuelana, new variety

WORKER

HEAD: Like that of the typical variety except that the mandibles are almost wholly black, with merely a reddish brown band just behind the black teeth along the apical edge.¹ The supraclypeus more uniformly hairy, with erect black hairs on its lower half as well as above the antennal sockets.

THORAX: Like that of typical variety.

LEGS: Like those of typical variety.

WINGS: With the color contrast and venational character of those of the typical variety but notably shorter. The number of hamuli per lower wing ranges from five to seven. Of 25 wings examined only two had as few as five hamuli and five as many as seven hamuli; the remaining 18 had six hamuli, an average of 6.12 hamuli.

ABDOMEN: Like that of typical variety.

MEASUREMENTS: Smaller than in typical variety. Length 6 to 7.5 mm., width of thorax about 2.5 mm.; length of forewing, including tegula, about 8.5 mm.

QUEEN

Unknown.

MALE

Unknown.

TYPE MATERIAL

The holotype, from Lagunita de Aroa, Venezuela, is in the United States National Museum. Paratypes are in the British Museum (Natural History) and in the American Museum of Natural History.

DISCUSSION

The variety *venezuelana* has the characteristic coloration of the wings that applies to typical *dimidiata*, but it can be differentiated at once by its small size and much shorter wing length. An additional distinction is the mainly black mandible of *venezuelana*, that of typical *dimidiata* being reddish

brown, but this distinction, while applying to the generality of specimens, is sometimes bridged by an aberrant specimen. The two varieties are finally distinguishable, it would seem, on the basis of such a relatively slight character as the presence or absence of erect black hairs on the lower half of the supraclypeus, as noted in the descriptions.

Nothing is known regarding the biology of *venezuelana*.

DISTRIBUTION

All of the specimens before me of this variety are from Venezuela, as follows:

VENEZUELA: Lagunita de Aroa, 2000 feet, Dec., 1910, including holotype (M. A. Carriker); mountains north of Caracas, July 1, 1926 (H. E. Box); Las Adjuntas, 959 meters (H. E. Box).

Trigona (Trigona) pallida variety
pallida (Latreille)

Apis pallida LATREILLE, 1804b, p. 177, pl. 13, fig. 14.

Trigona pallida, LATREILLE, 1809, p. 183.

Trigona pallida, LATREILLE, "1811"b, p. 294, pl. 20, figs. 6 and F.

Melipona pallida, LAMARCK, 1817, p. 53.

Trigona pallida, PERTY, [1833], p. 26.

Melipona pallida, LAMARCK, 1835, p. 273.

Melipona pallida, LEPELETIER, 1836, p. 432.

Trigona pallida, SPINOLA, 1840, pp. 124, 128, pl. 2, fig. 6.

Trigona pallida, ERICHSON, 1841, p. 219.

Melipona pallida, ERICHSON, 1848, p. 592.

? *Trigona pallida*, BLANCHARD, 1849a, p. 86.

Trigona mellea F. SMITH, 1863a, p. 510, pl. 20, figs. 4, 11.

? *Trigona pallida*, GRIBODO, 1895, pp. 200-201.

Melipona mellea, DALLA TORRE, 1896, p. 580.

Melipona pallida, DALLA TORRE, 1896, p. 582.

Trigona kohli FRIESE, 1900a, p. 387.

Melipona kohli, DUCKE, 1901, p. 65.

Melipona kohli, DUCKE, 1902a, p. 420.

Melipona (Trigona) kohlii, DUCKE, 1902b, pp. 290, 303.

Trigona Kohli, DUCKE, 1907, p. 89.

Trigona kohli, MARIANNO, 1911, pp. 112-113.

Trigona pallida, COCKERELL, 1912b, p. 61.

Trigona pallida, COCKERELL, 1913a, p. 10.

Trigona pallida, WHEELER, 1913, p. 3 (identified by T. D. A. Cockerell).

Melipona Kohli, RUDOW, 1914, pp. 241-242, fig. 12.

Melipona Kohli, DUCKE, 1916, opposite p. 28, pp. 127-129 (in part).

Trigona pallida, COCKERELL, 1920c, pp. 460, 463-464.

¹ This melanistic extreme is approximated by specimens from Satipo, Peru, which in other respects align themselves with typical *dimidiata*.

Trigona pallida, LUTZ AND COCKERELL, 1920, pp. 499-500.

? *Trigona pallida*, HERBST, 1921, p. 102.

Trigona pallida, COCKERELL, 1922, p. 8.

Trigona kohli, WHEELER, 1923, p. 122.

Trigona kohli, LUTZ, 1924a, pp. 210, 216 (identified by H. Friese).

Melipona kohli, DUCKE, 1925, pp. 344, 354, 415-416 (in part).

Trigona pallida, SCHWARZ, 1932a, pp. 238, 391.

Trigona pallida, SCHWARZ, 1932b, pp. 552-553.

Trigona pallida, RAU, 1933, pp. 16, 37-38 (identified by H. F. Schwarz).

Trigona pallida subspecies *pallida*, SCHWARZ, 1934, pp. 4, 11-12.

Trigona kohli, MAIDL, 1934, p. 392.

Trigona (*Trigona*) *pallida* variety *pallida*, SCHWARZ, 1938, pp. 437, 443, 462-464, pl. 52, figs. A, A1, B, F, pl. 53, figs. A, B, C.

Trigona (*Trigona*) *pallida* variety *pallida*, SCHWARZ, 1940, p. 5.

Melipona kohli, R. VON IHERING, 1940, p. 297.

Trigona pallida, ESSIG, 1942, p. 721.

Melipona kohli, DUCKE, 1945, opposite p. 24, pp. 96-97 (in part).

Trigona pallida pallida, MICHENER, 1946, p. 195.

WORKER

DIAGNOSTIC CHARACTERS: Ferruginous. Mandible five toothed. Length of malar space about that of width of flagellum. Length of clypeus not quite one-half its greatest width. Labrum with two feeble prominences. Erect fulvous hairs on clypeus, supraclypeus, and scape. Hind tibiae with an inwardly placed angle posteriorly at the apex. The apex of the hind metatarsi posteriorly rounded to subrectangular. Wings almost hyaline to diluted yellowish gray, subtransparent.

HEAD (FIG. 37A): Ferruginous to honey colored. The facial quadrangle moderately wide, the distance between the compound eyes at the level just below the anterior ocellus being a little less (in the proportion of about 9 to 10) than the distance from the anterior ocellus to the apex of the clypeus. The compound eyes slightly convergent below, the distance that separates them at their level of greatest approximation (below) being very nearly four-fifths that of their divergence at the level just below the anterior ocellus. The clypeus and supraclypeus raised slightly above the sides of the face, of even surface and without a median fossa.

The length of the clypeus not quite one-half its greatest width measured from one antero-lateral extremity to the other; each antero-lateral extremity of the clypeus separated from the nearest compound eye by less than one-half the width of the flagellum. The labrum with two more or less distinct tubercles (fig. 37A1). The mandibles armed with five teeth, the two innermost small. The malar space, measured from the lower extremity of the eye to the middle of the base of the mandible, approximates the width of the flagellum. The distance between the lateral ocelli subequal to that separating each lateral ocellus from the nearest compound eye. The carina behind the ocelli low, blunt, and ill defined. Clypeus, front, vertex, and sides of face rather densely covered with silvery gray, appressed, microscopic hairs; the upper two-thirds of the genal area silvery gray pruinose (or in some positions yellowish to olivaceous). All the erect hairs of the head fulvous, those on the clypeus and supraclypeus long, longer than the hairs on the scape (the latter somewhat variable in length, usually longer or about as long as the scape is wide) and about as conspicuous as the somewhat sparse erect hairs on the front. The hairs of the vertex, lower one-third of genal area, and inferior margin of mandibles longer. The head completely, or nearly completely, ferruginous to honey colored, with the following parts black: teeth of mandibles, the ocelli sometimes, the apical tip of the scape posteriorly, the flagellum above except for the often ferruginous apical joint. The eyes in life light green (Ducke, 1916, p. 128; 1925, p. 416; 1945, p. 97), but in mounted specimens they vary considerably, being largely yellow, or mottled with black or predominantly dark.

THORAX: Bright ferruginous like the head, the mesonotum often being a shade deeper than are the mesopleura and scutellum. These parts and the sides of the propodeum of somewhat subdued sheen due to the presence of dense silvery gray tomentum in addition to the erect simple hairs, which over the dorsal area and upper part of the mesopleura are fulvous but tend sometimes to become silvery gray towards the lower half of the mesopleura and the under side of the thorax; the erect hairs interspersed among the to-

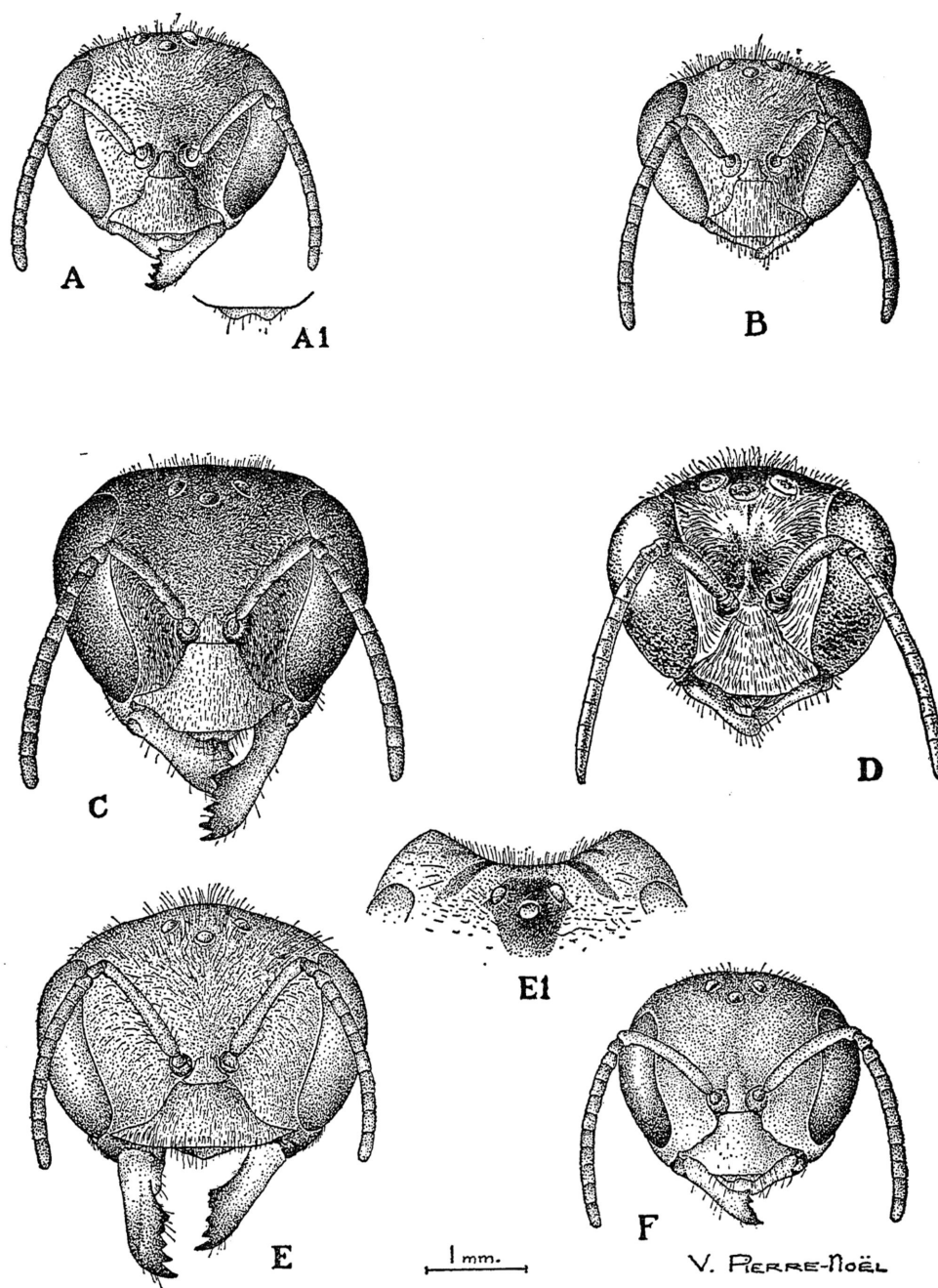


FIG. 37. Head of worker (A, with A1 representing the labrum), male (B), and queen (F) of *Trigona (Trigona) pallida* variety *pallida* (Latreille); worker (C) and male (D) of *Trigona (Trigona) williana* Friese; worker (E) of *Trigona (Trigona) dal-latorreana* Friese, with E1 illustrating aberration of this species with characteristic markings on head viewed from above. Drawings by V. Pierre-Noël.

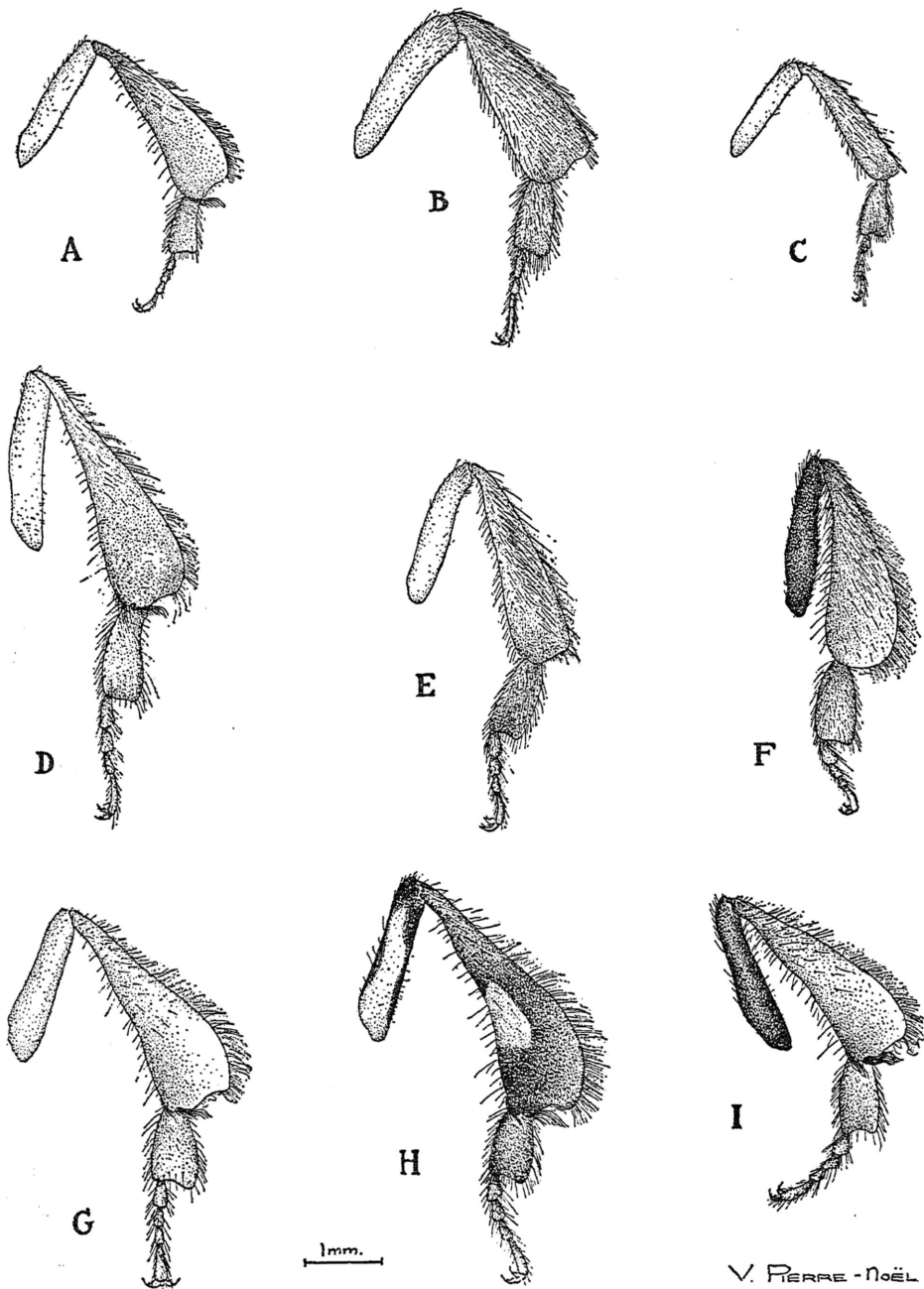


FIG. 38. Hind tibia, metatarsus, and small tarsal joints of worker (A), queen (B), male (C) of *Trigona (Trigona) pallida* variety *pallida* (Latreille); worker (D) and male (E) of *Trigona (Trigona) williana* Friese; male (F) and worker (I) of *Trigona (Trigona) ruficrus* Latreille; light and dark extremes (G and H, respectively) in the worker of *Trigona (Trigona) dallatorreana* Friese. Drawings by V. Pierre-Noël.

mentum on the sides of the propodeum also mostly silvery gray. The prothorax long and collar-like, covered densely with silvery gray microscopic hairs like those on the face, its length perceptibly greater than that of the scutellum. The relative length of the hairs of the thorax as indicated in the description of the worker of the subgenus *Trigona*.

LEGS: Of a bright ferruginous. The hind tibiae (figs. 38A, 41A) clavate in outline, wider at the apex than at the base, their anterior lateral contour barely emarginate to straight; posterior lateral contour strongly convex; their apex with an inconspicuous angle anteriorly that bears the tibial comb; beyond this angle there is a slight bulge in the apical contour followed by an emargination that results in a somewhat inwardly placed angle where this emargination encounters the posterior contour of the joint. The outer face of the hind tibiae approximating a flattened condition on its basal three-fifths, particularly posteriorly, and lightly depressed on its apical two-fifths. The flattened area margining the under side of the hind tibiae posteriorly about one-third of the width of the tibiae towards the apex. The hind metatarsi a little more than one-half the maximum width of the hind tibiae, their apex posteriorly rounded to subrectangular. The hairs of the leg predominantly more or less fulvous with the following relatively minor exceptions: the dense fringe of very microscopic whitish hairs usually traceable on the under side of the femora, the silvery gray plumose hairs on the outer face of middle tibiae and basal region of corresponding metatarsi, the microscopic but stubby silvery gray hairs over the raised portion of the under side of the hind tibiae and over the adjacent apical region of the under side of the hind femora. The suboval bristleless patch at the base of the under side of the hind metatarsi often appears bare, as the sericeous hairs covering it are exceedingly fine and easily obliterated by moisture; as a result this patch usually gives the impression of being fulvous like the rest of the joint. The relative length of the hairs and their distribution as indicated in the description of the worker of the subgenus *Trigona*.

WINGS: Of a uniform, almost hyaline to diluted yellowish gray stain, subtransparent;

the median cell not darker than the other cells. The venation and stigma more or less ferruginous, sometimes even a little fuscous; the tegulae usually a barely paler ferruginous. The transverse cubital veins are hardly or not at all traceable. The first discoidal cell about three-fourths the length of the marginal cell. Number of hamuli ranges from five to seven, but is usually only five. Of 160 wings examined 130 had five hamuli, 28 had six hamuli,¹ and only two had seven hamuli, an average of 5.20.

ABDOMEN: Wholly or predominantly concolorous with the rest of the body, now and then a little darkened on the apical segments, and in extreme cases largely black; somewhat narrower than the thorax; the tergites rather fully exposed instead of telescoped, tergites 5 and 6 tending to be vertical in position. The hairs on the tergites pale, short, and few. The appressed hairs occurring sparsely along the apex of tergites 2 and 3 are so diminutive and scant that they are easily overlooked, and in some cases indeed they appear to be absent on at least tergite 2. Tergite 4 with a few erect hairs; tergites 5 and 6 only a little more hirsute. The tufts of fulvous to pale hairs at the middle of the apex of the several sternites are supplemented on each side of sternites 3 to 5 by glistening dense silvery gray sericeous patches.

MEASUREMENTS: Length 4.5 to 6 mm.; width of thorax 1.75 to 2 mm.; length of forewing, including tegula, about 6 to 6.25 mm.

QUEEN (GRAVID)²

HEAD (FIG. 37F): A little wider than the mesonotum but not nearly so wide as the distance between the outer rim of one of the tegulae and the outer rim of the other. The facial quadrangle wide, the distance between the compound eyes at the level just below the middle ocellus about equal to the distance that separates the middle ocellus from the apical margin of the clypeus. The eyes a little convergent below, barely shorter but a little more distinctly narrow than those of the

¹ The percentage of specimens having six or more hamuli was especially high in a series from the Kuyuwini River, British Guiana.

² Description based on a single specimen from Barro Colorado Island, Canal Zone.

worker. Eyes not in the least hairy. The clypeus gently arched; raised, like the supraclypeus, a little above the level of the sides of the face and of smooth surface. The width of the clypeus, measured from one apico-lateral extremity to the other, about twice its length. The labrum rather strongly bituberculate. The dentition of the mandible indistinct, the outermost and the two innermost teeth of the apex being the only ones clearly demarked. The length of the malar space somewhat greater than the width of the flagellum and roughly about one-sixth as long as the eye. The ocelli small and remote from the eye, the distance from the summit of the eye to the nearest lateral ocellus being about one and one-half times that separating each lateral ocellus from the other lateral ocellus. The carina behind the ocelli very feeble, barely traceable. The entire head shiny, little concealed by the exceedingly microscopic silvery gray hairs that cover all areas except the lower one-third of the genal area, where there are a few erect fulvous hairs. The hairs fringing the mandibles below also fulvous and long, rather longer than the mandible is wide at the base. A few hairs, fulvous to silvery gray, on the labrum and on the vertex, but no erect hairs whatever on the clypeus, sides of face, front, or upper two-thirds of genal area. The scape, on the other hand, with very fine erect pale hairs that are shorter than the scape is wide. Coloration approximates that of the worker. The eyes and the apical edge of the mandibles are dark. In the specimen on which this description is based the sides of the face, the front, the genal area, and the malar space are a little more reddish than the pale ferruginous to yellowish clypeus, supraclypeus, scape, under side of flagellum, labrum, and basal two-thirds of mandibles (but these differences in hue may be individual rather than specific). The flagellum about twice the length of the scape and of about the same width.

THORAX: Rather shiny, nearly concolorous with the head, being wholly ferruginous to honey colored. Its width greater than that of the worker. The mesonotum virtually as wide as the mesonotum plus scutellum are long. The mesonotum and pleura (except below) devoid or virtually devoid of erect

hairs, being covered with short, silvery gray appressed hairs, but the scutellum with rather conspicuously long fulvous hairs.

LEGS: Rather uniformly ferruginous. The hind tibiae (fig. 38B) about as long as the combined length of the hind trochanters and femora, clavate to triangular in outline, wider apically than basally,¹ their apex feebly rounded anteriorly, and with an obtuse angle posteriorly. The hind metatarsi about three-fifths as wide as the associated tibiae at the apex, rather parallel sided throughout their length, although briefly convergent at base, their length (measured along the inner face) a little less than that of the combined small joints; the posterior apical angle of hind metatarsi subrectangular; the inner face of the hind metatarsi with fulvous bristles along the apical edge, otherwise rather uniformly covered with soft, yellowish golden hairs that are rather even in length. Hairs of similar character and color on the inner face of the metatarsi of the anterior and middle legs. The other hairs of the legs also yellowish (except for the short fringing hairs on the under side of the femora, particularly the hind pair, which are more silvery gray) and for the most part semi-erect to appressed. The femora are moderately hairy on their outer (anterior) side and particularly their under side, more glabrous on their inner (posterior) face. The hairs on the outer face of all the tibiae (including the hind pair) relatively dense, and, although they tend to be progressively longer from the fore tibiae to the hind tibiae, the contrast in length between those on the outer face of the fore tibiae and those on the outer face of the middle tibiae is not so marked as in the worker, and the plumose hairs that are present on the outer face of the middle tibiae of that caste are absent in the corresponding area of the queen. The hairs are longer posteriorly than anteriorly on all of the tibiae, and this applies also to the posterior lateral fringes on the several metatarsi. The fringe along the posterior lateral rim of the hind tibiae with-

¹ Ducke's observations (1916, p. 127; 1925, p. 415; 1945, p. 96) are at variance with my own. He speaks of the hind tibiae of the queen as "somewhat narrower than in the worker," whereas, according to my measurement, they are, at their widest, nearly one-quarter again as wide as those of the worker.

out traceable admixture of plumose hairs.

WINGS: About the same length as those of the worker (relative to the body length much shorter, attaining only the apex of tergite 2 of the abdomen) and like them of a uniform, almost hyaline to diluted yellowish gray stain. The number of hamuli per lower wing five. The tegulae of a slightly paler ferruginous than the venation of the wings.

ABDOMEN: Ferruginous, shiny, particularly so on tergites 1 and 2, which are virtually glabrous. The hairs on tergites 3 to 6 fine and soft, silvery gray to, in some lights, fulvous, short and, although increasing in length from base to apex on each of these tergites, nevertheless not notably longer from tergite to tergite when hairs correspondingly placed are compared. No clearly traceable punctuation of the tergites. Erect fulvous hairs on the apical half of the successive sternites.

MEASUREMENTS: Length about 8.5 mm. (of which the distended abdomen occupies about 5.5 mm.); width of thorax about 2.75 mm.; length of forewing, including tegula, about 6 mm.

MALE

HEAD (FIG. 37B): As is the rest of the body, bright ferruginous. The facial quadrangle narrower than in the worker. The distance from one eye to the other at their level of closest approximation is about three-fifths of the length of the eye, whereas in the worker the shortest distance between the eyes is about five-sixths of the length of the eye. The clypeus and supraclypeus barely more prominent than the sides of the face; the apico-lateral extremities of the clypeus subrectangular, grazing or almost grazing the rim of the eye; the length of the clypeus very nearly two-thirds its greatest width. The labrum much less distinctly bituberculate than is the case in the worker, the very feeble eminences barely discernible. The mandible shaped somewhat like a thumb, bluntly pointed at the apex (rather than inwardly receding) and edentate. The malar space virtually obsolete, the inner angle at the base of the mandible grazing the rim of the eye. The distance between the lateral ocelli a little greater than that between each lateral ocellus and the nearest compound eye. The carina behind the lateral ocelli low, blunt,

and ill defined. The head about as moderately hirsute as that of the worker. The dense appressed microscopic hairs on the clypeus, sides of face, front, vertex, and genal area (densely covering all but the lower extremity of this area) silvery gray. The erect hairs silvery gray to fulvous; those of the clypeus long and rather evenly distributed, notably longer than the inconspicuous hairs on the scape and rather longer, too, than the hairs on the front; the hairs on the vertex, lower margin of mandibles, and lower extremity of genal area as a rule only a little longer than those of the clypeus. The scape ferruginous as is the rest of the head, and the flagellum more or less ferruginous below but black above.

THORAX: Bright ferruginous as is the head. The hairs of the mesonotum very short, for the most part appressed or semi-appressed and silvery gray as are the slightly longer and more erect hairs of the mesopleura. The long erect hairs of the scutellum, which tend to fulvous, completely dwarf the hairs of the mesonotum and of the mesopleura and are intermixed with silvery gray tomentum, which is especially dense also in the region on each side of the hairless middle region of the propodeum.

LEGS: Concolorous with the head and thorax. The hind tibiae (fig. 38C) narrow, almost straight (a little convex towards the apex) along their anterior lateral contour, somewhat convex along their posterior lateral contour; the posterior part of the outer face rather flattened and, towards the apex especially, even somewhat concave; the contour of the apex of these tibiae somewhat irregularly rounded; their greatest width (near the apex) about two-thirds that of the conspecific worker at the corresponding level. The hind metatarsi only a shade narrower than the associated tibiae, being fully four-fifths their width, the posterior apical extremity of these metatarsi subrectangular to rounded. The hairs predominantly more or less fulvous, those on the under side of the trochanters, the very microscopic fringes on the under side of the femora, the microscopic but stubby hairs down the raised area on the under side of the hind tibiae and the adjacent region at the apex of the under side of the hind femora, and the small area of appressed

sericeous hairs at the base of the under side of the hind metatarsi all tending to be more or less whitish to silvery gray, although the differentiation from the more fulvous hairs is often very slight. Judging from the limited number of specimens before me, there are no or few plumose hairs on the outer face or even the posterior lateral contour of the middle tibiae, and the posterior lateral fringe of the

usually only a few inconspicuous appressed hairs along its apex; tergites 4 to 6 with erect fulvous hairs of intermediate length sparsely present; tergite 7 thinly fringed with moderately long hairs along its apex. The sericeous hairs of the sternites silvery white. For the structure of the sternites and genitalia, see figure 39.

MEASUREMENTS: Length 5 to 5.5 mm.;

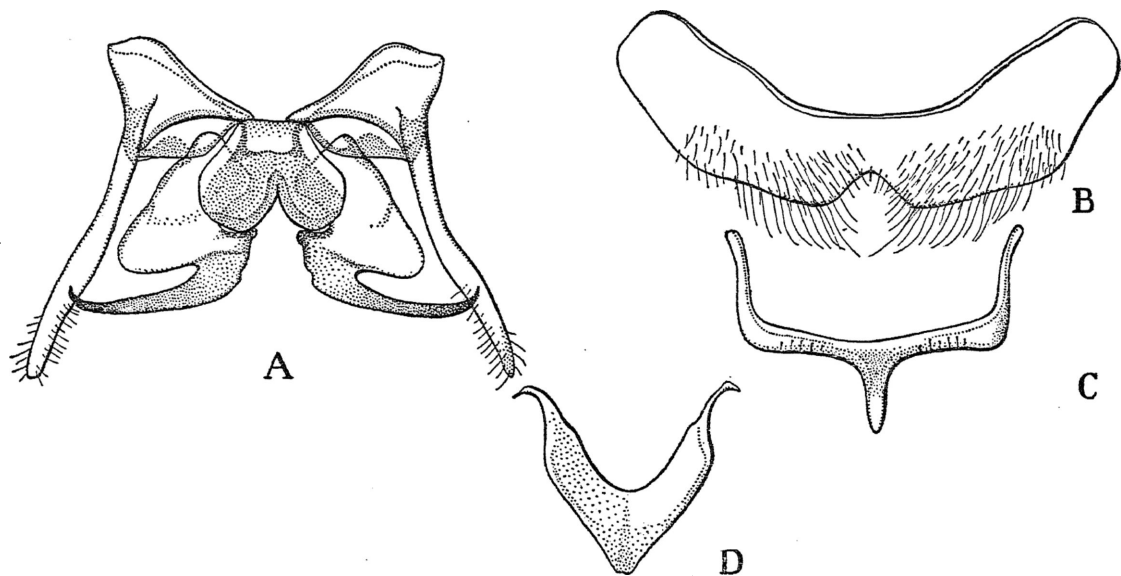


FIG. 39. Abdominal parts of male of *Trigona* (*Trigona*) *pallida* variety *pallida* (Latreille). A. Genitalia (chitinized parts only). B. Sternite 5. C. Sternite 6. D. Sternite 7. All based on a specimen from Balboa, Canal Zone. Drawings by Shirley H. Risser.

hind tibiae usually consists entirely or largely of scanty simple hairs. The distribution of the simple fulvous hairs in general and the relative length of these hairs approximately as indicated in the generalized description of the male of subgenus *Trigona*.

WINGS: Like those of the worker, almost hyaline to diluted yellowish gray, subtransparent; the median cell no darker than the other cells. The venation and stigma in the few specimens available with a tendency to be a little darker than is usual in the worker, slightly fuscous rather than ferruginous. Of 12 wings examined, 11 had five hamuli and one had four hamuli, an average of 4.92.

ABDOMEN: More or less concolorous with the other body parts and approximating the thorax in width. Tergites 1 and 2 bare; tergite 3 also approximately hairless with

width of thorax 1.75 to 2 mm.; length of forewing, including tegula, 5.75 to 6.25 mm.

TYPE MATERIAL

What is believed to be the type of *pallida*, described from French Guiana, is in the museum at Oxford University.

DISCUSSION

It has been not unusual for authors to interpret as Latreille's *pallida* the insect that Klug described as *testacea* and to follow Friese in designating as *kohli* what is true *pallida*. There can be no doubt, I think, that *pallida* is the insect with five-toothed mandibles and of ferruginous coloration to which Cockerell (1920c, pp. 463-464) restored the name as the true claimant. The correctness of Cockerell's interpretation was confirmed

by an examination which he subsequently made (1922, p. 8) of Latreille's type of *pallida* at Oxford University. This specimen, although headless, is unquestionably the same as Friese's *kohli*. In addition, I had opportunity to see during my own visit to Oxford a specimen labeled *pallida* in handwriting thought to be that of Lepeletier. This insect, too, accords with the interpretation of *pallida* here adopted. If further proof is needed to substantiate this interpretation, it is found in Latreille's original description, which states that *pallida* differs from *amalihea* and *ruficrus* only by virtue of its pale yellowish red color and its slightly smaller size. Finally Latreille ("1811"b, pl. 20, fig. F) supplied a drawing of the mandibles of *pallida*, which distinctly shows a quinque-dentate condition and should dispel once for all the impression that *pallida* is the structurally very different insect described by Klug as *testacea*.

Cockerell (1920c, pp. 463-464) called attention to the fact that *kohli* is identical with *pallida* as understood by F. Smith. There is a specimen identified by Smith as *pallida* in Professor Cockerell's collection¹ and among the specimens in the British Museum designated *pallida* are two labeled "Smith Coll. pres. by Mrs. Farren White 99-303." This label appears also on four specimens in the British Museum that have been identified, presumably by Smith, as *mellea*. The type of *mellea* I could not locate, but the fact that the four specimens are from the Smith collection and that one of them, in addition to the scientific name, bears the popular name "Cutia o de purga," which Smith associated with *mellea*, and the further fact that the specimens are from Brazil from which *mellea* was described lead to the conclusion that the specimens are part of the original material of *mellea*. If so, *mellea* is scarcely separable from *pallida*. The specimens are a little larger than is usual in *pallida*, but I think the impression of size is largely due to artificial lengthening of the abdomen, which is rather crushed and distorted in these specimens and perhaps misled Smith into describing the abdomen of *mellea* as "elongate." Certainly the insects are much nearer to the average size of *pallida*

than they are to the much larger *williana*. Indeed, the length recorded by Smith, "3 lines," is somewhat less than the maximum size, 6.5 mm., given by Ducke for *kohli*. The description of *mellea* applies well to *pallida* and strengthens the impression that *mellea*, like *kohli*, is merely a synonym of *pallida*.

About one-half of the specimens of *pallida* collected on the Kuyuwini River in British Guiana are assignable without hesitation to the typical variety. The remainder show varying degrees of obscuration of the abdomen, usually beyond the first, or the first two tergites. It is not altogether exceptional to find in typical *pallida* some darkening of the apical segments of the abdomen, but these specimens are unusual in that in extreme cases several of the tergites (and frequently likewise the sternites) are predominantly or wholly black. Were it not for the presence in the series of specimens that, in contrast, have the usual honey-colored abdomen commonly associated with typical *pallida*, I should be inclined to regard the representatives from the Kuyuwini River as a distinct variety.

The wing length of typical *pallida* shows some variability, but most specimens tend to have a little shorter wing length than have the variety *ferricauda* Cockerell and the new species *chanchamayoënsis*.

Ducke (1902a, p. 420; 1902b, p. 303) recorded a nest of this species in the trunk of a tree in a primeval forest, and in his later account (1925, p. 415) summarized the nesting places as hollow trees, termite nests in hollow trees, or the exposed nests of arboreal termites. The inclusion of the last-mentioned nesting site was based on the observation of Silvestri, who reported a colony located in the exposed nest of a termite. But the bees' nest in question (referred by Silvestri to *kohli*, here considered a synonym of *pallida*) was, it seems to me, more probably the work of the closely related *chanchamayoënsis*. However, Rudow (1914, pp. 241-242) also reported a nest of "*Kohli*" from an exposed termite structure.

The association of *pallida* with termites still persists even beyond South America, for C. D. Michener in a letter to me reported the following concerning this species, a nest of which he located on the Río Pescado arm of

¹ This specimen was kindly donated to the American Museum by Professor Cockerell.

Gatun Lake, Canal Zone: "Nest in horizontal dead log lying on ground. Log thoroughly infested with termites and largely covered by their nest, so that bee nest must have been among the termite galleries. Entrance of nest consists of grayish black material which is rather hard. Entrance tube one inch in diameter, about one inch long, round in cross section, projecting from the side of the log."

In the State of Pará, Brazil, according to Ducke (1901, p. 65; 1902b, p. 303), this bee visits very many different flowers, especially *Urena lobata* and *Waltheria americana*. Banana blossoms and water lilies for their nectar proved attractive to *pallida* on Barro Colorado Island in the Canal Zone (Rau, 1933, pp. 37-38).

In addition to flowers, *pallida* is partial also to other things. In British Guiana it was collected by H. Crampton as it flew to jam, and in that country Lutz took it on the carcass of a monkey and also of a snake. Apparently the bees not only sucked the fluids of the dead animals "but also carried off small bits of the flesh" (cited by Cockerell, 1920c, pp. 460, 463). The excrement of animals, too, lures this species (Rau, 1933, p. 38), doubtless as building material for the nest.

In the Canal Zone *pallida* has been observed loading itself with oily substances. The first one to note this curious activity was William Morton Wheeler, whose graphic account (1913, p. 3) is worthy of quotation in full: "This light-yellow species was common at a spot near Gatun, C. Z. on the relocated Panama R. R., where it exhibited a most extraordinary habit. At a wet ravine on one side of the track a barrel of black crude oil (with asphalt basis) had been placed as a supply for the men employed in exterminating mosquito larvae and pupae, and near it was a bucket which had been filled from the barrel. Perched around the rim of this bucket and crawling about the leaking spigot in the flat end of the barrel were great numbers of the bees, loading themselves with the oil! They could be seen collecting the oil with their fore legs and then transferring it to their dilated hind tibiae. In this occupation many had succeeded in daubing their whole body, including the wings, with the sticky, strong-smelling substance, and at first sight

seemed to be trying to convert themselves into pitch-black *Trigonas*. They were not, of course, really endeavoring to adopt the prevailing style of coloration among the Central American species, but were merely collecting the oil for the purpose of kneading it up with their own waxy secretions, to form the cerumen with which they build their honey pots, brood-combs and nest entrances."

Rau (1933, p. 37) observed dozens of *pallida* specimens throughout the morning "loading their pollen baskets with the heavy grease from the cog-wheels of the hoist at the boat landing" on Barro Colorado Island.

On this island I, too, had opportunity to note on several occasions the partiality of *pallida* for oily and greasy substances. A gasoline engine hidden under an inverted wooden box was a rendezvous for many *pallida* workers that entered through a small opening in the box to obtain the treasures of grease and gasoline available within. One day I witnessed a curious fracas between individual workers that had visited the dark interior of the box and that had issued forth bedabbled with the sticky substance of their search. A number of them were flying about in great agitation with adversary gripping adversary in this aerial battle and then falling to the ground, there to continue the struggle like evenly matched wrestlers. So intent did these pairs of gladiators seem in their unexplained hostility that they still clutched each other rigidly with their mandibles even after being transferred to the killing bottle. And yet, it is very likely that they were all members of the same nest and that the combat was therefore sororicidal (Schwarz, 1932b, p. 553).

Because of its association with termites, this bee shares with certain other bees of similar habit the popular name "cupira," meaning termite bee or nest in termite structure (Ducke, 1916, opposite p. 28; 1925, p. 344; 1945, opposite p. 24).

DISTRIBUTION

Trigona pallida was recorded by Latreille (1811b, p. 294) from French Guiana. Subsequently under the name of *kohli* it was re-described by Friese on the basis of specimens obtained in Peru, Colombia, French Guiana, Surinam, and Brazil. It has been claimed by

Gribodo (1895, p. 201)¹ that it occurs in Chile, but this is disputed by Herbst (1921, p. 102). Cockerell (1920c, pp. 463-464) recorded it from British Guiana and listed also localities in the Panama region. It is an abundant species on Barro Colorado Island, Canal Zone, occurring in the neighborhood of the laboratory, on the Drayton Trail and the Wheeler Trail, at Redwood House, and at the Rear Lighthouse. The northernmost known range of the species seems to be Honduras, from which there are several representatives in the present collections. Ducke (1925, pp. 415-416) stated that it is "Abundant in the eastern Hyläa, extending southward to the bordering regions of north-eastern and central Brazil."

Ducke listed various localities in the State of Pará where it occurs and included also one or more localities in the Brazilian States of Maranhão, Goyaz, and Matto Grosso (the last-mentioned on the authority of Silvestri²). Cockerell (1912b, p. 61) had likewise recorded a specimen from Matto Grosso, collected by Mann and Baker "on the Rio Madeira nearly opposite mouth of Rio Abuná."

In the collections before me there are representatives from the following localities:

HONDURAS: Tegucigalpa, March 30, 1917 (F. J. Dyer); Corocito, Apr. 3, 1924 (J. Bequaert); Prieta, Apr. 7, 1924 (J. Bequaert); Cecilia (W. M. Mann); Maloa, May, 1924 (W. M. Mann); Lombardia, male (W. M. Mann).

COSTA RICA: Zent, March, 1924 (W. M. Mann); Suretka, Province of Limon, Apr. 26, 1924 (J. C. Bradley).

CANAL ZONE: Alhajuela, May 18, 1909 (A. H. Jennings), and May 28, 1912 (A. Busck); Paraiso, Feb. 2, 1911 (A. Busck); Gatun, Nov. 11, 1911 (W. M. Wheeler); Balboa, male, Aug. 21, 1914, and Nov. 20, 1914 (T. Hallinan); Empire, male, Aug. 30, 1914 (T. Hallinan); Arraiján Trail, Dec. 16, 1914, and Jan. 1, 1915 (T. Hallinan); Red Tank, April 10, 1923 (W. M. Wheeler); Barro Colorado Island, Nov. 12-18, 1923 (F. E. Lutz), Apr. 4, 1924, queen and workers (J. C. Bradley), July 16, 1924, and July 30, 1924 (N. Banks), Dec. 19-30, 1928 (C. H. Curran), Nov.-Dec., 1930 (F. E. Lutz, E. I. Huntington, H. F. Schwarz),

March 18, 1936 (F. E. Lutz); Chiva Chiva Trail, Nov. 18, 1923 (F. E. Lutz), Nov. 24, 1930 (H. F. Schwarz), March 11, 1933 (H. F. Schwarz); Gamboa, July 9, 1924 (N. Banks); Frijoles, July 10, 1924 (N. Banks); Marajal, near Colon, July 10-11, 1924 (W. M. Wheeler); Corozal, Jan. 16-19, 1929 (C. H. Curran).

PANAMA: Río Trinidad, March 16, 1912 (A. Busck); La Chorrera, April 12, 1912 (A. Busck); Porto Bello Trail, May 30, 1915 (T. Hallinan); Las Sabanas, Nov. 17, 1923 (F. E. Lutz).

COLOMBIA: Department of Boyacá: Muzo, 900 meters, 1936, males and workers (J. Bequaert).

BRITISH GUIANA: Rockstone, July 9, 1911 (F. E. Lutz), May 8, 1913 (G. E. Bodkin), and June 26, 1927 (Cornell Univ. Exped.); Tukeit, July 19, 1911 (F. E. Lutz); Kaieteur, Aug. 5, 1911 (F. E. Lutz); Kuyuwini River, Nov. 22, 1937 (W. G. Hassler); Tumatumari, July, 1913 (Leo E. Miller); Waratuk, Feb. 11, 1921 (W. Beebe collection).

SURINAM: Paramaribo, April 4, 1927; Sint Barbara Pln., Surinam River, April 12, 1927; Moengo, Boven Cottica River, May 14, 1927; Kwakoepron, Saramacca River, June 10, 1927. (All of the above Surinam specimens were collected by the expedition of Cornell Univ.)

BRAZIL: State of Pará: Santarem (H. H. Smith); Prata, June 31 and July 2, 1919 (H. Parish). State of Goyaz: Specimens lent by Cornell Univ.

Trigona (Trigona) pallida variety
muzoënsis, new variety

WORKER

Unknown.

QUEEN

Unknown.

MALE

Structurally like the male of typical *pallida*, but predominantly black instead of honey colored.

HEAD: Much like that of worker of *pallida* variety *ferricauda* (male of *ferricauda* unknown), black except for honey-colored clypeus, supraclypeus, mandibles, labrum, malar space, sometimes lower extremity of sides of face, and scape at least in front. Flagellum for the most part black, with sometimes traces of dull brown on the under side. The hairs of the vertex sometimes a little sooty.

THORAX: More extensively black than in the variety *ferricauda* or in the closely allied *chanchamayoënsis*, not only the entire mesonotum being black but also the sides of the

¹ It is possible that Gribodo's *pallida* is *testacea*.

² It seems to me likely that the specimens that Silvestri reported from Matto Grosso are *chanchamayoënsis* rather than *pallida*.

thorax and the propodeum; only the following parts more or less honey colored to ferruginous: prothorax (the pronotum, however, often sooty to black), the tubercles, tegulae, axillae (rarely), scutellum, and a narrow band immediately below the scutellum.

LEGS: Variable in respect to the extent to which the light coloration is invaded or replaced by black. Usually at least the coxae and trochanters are largely or wholly honey colored, but the more apical joints, too, may be incompletely darkened. The femora, tibiae, and tarsi are largely deep yellowish brown to blackish, with usually somewhat lighter areas on the femora basally, on the tibiae basally and apically, and on the hind tibiae anteriorly. The hairs on the under side of the trochanters and the fine hairs fringing the femora beneath are pale, but the hairs on the other parts of the legs are for the most part brownish to blackish, especially so in the darker specimens.

WINGS: Hyaline to subhyaline, with fuscous venation and stigma; the upper half of the first transverse cubital vein fairly defined, the second transverse cubital feebly. The first discoidal cell about three-fourths as long as marginal. Number of hamuli in each hind wing variable from five to six. Of 24 wings counted, 22 had five hamuli, two had six hamuli, or an average of 5.08.

ABDOMEN: Darker in coloration than in the typical variety (the Kuyuwini River specimens excepted) and in the other varieties, ranging from more or less clouded yellowish brown in the less melanistic specimens to blackish brown in the darker examples, the dorsal aspect being somewhat darker than the ventral.

MEASUREMENTS: Length 5 to 6 mm.; width of thorax 1.75 to 2 mm.; length of forewing, including tegula, 5.75 to 6.25 mm.

TYPE MATERIAL

Holotype and paratypes at Museum of Comparative Zoölogy; paratypes at the American Museum of Natural History.

DISCUSSION

The variety *muzoënsis* represents the extreme of melanism in a species the other representatives of which are either wholly or predominantly ferruginous. Belying its

specific name, it departs in its coloration so emphatically from typical *pallida* that individual specimens, at least, would group themselves with the dark species of the subgenus *Trigona*, with which in other respects they have no very close affiliation. Unfortunately there are no workers among the type material, and for this reason *muzoënsis* could not be included in the key to the workers of the subgenus *Trigona*.

This variety is closest to *ferricauda*, particularly in respect to the maculation of its head, which is very similar to that of the worker of *ferricauda*. It is very improbable that the present variety is the unknown male of *ferricauda*, because of the greater extent of its black areas and the occurrence of black in parts where the *ferricauda* worker is ferruginous.

DISTRIBUTION

Known as yet only from Muzo, Department of Boyaca, at 900 meters, Colombia, where it was collected in 1936 by J. Bequaert. At the same locality Bequaert obtained also specimens of the typical variety.

Trigona (Trigona) pallida variety *ferricauda* Cockerell

Trigona ferricauda COCKERELL, 1917, p. 127.

Trigona pallida subspecies *ferricauda*, RAU, 1933, pp. 16, 38 (identified by H. F. Schwarz).

Trigona pallida subspecies *ferricauda*, SCHWARZ, 1934, pp. 4, 12.

WORKER

HEAD: Structurally like that of typical *pallida*. The erect hairs as in the typical form fulvous, but those on the scape fine and short, not so long as the scape is wide and conspicuously shorter than the hairs on the clypeus, supraclypeus, and front, and the still longer hairs of the vertex, lower one-third of genal area, and inferior margin of mandibles. Differs from the typical variety in having only the following parts ferruginous to honey colored: clypeus, supraclypeal area, lower corners of face (the last sometimes obscurely), labrum, mandibles exclusive of apex and the lower one-half of the genal area; the other parts of the head are black. The antennal sockets ferruginous and the scape ferruginous except for a black mark posteriorly at the apex; flagellum more or less dark-

ened above, ferruginous below, except for the apical joints, which tend to be ferruginous both above and below.

THORAX: Mesonotum black, with narrow ferruginous lateral and hind margins (more emphatic in the Panamanian specimens before me than in the Ecuadoran specimens), and sometimes faintly discernible also are two very narrow and posteriorly diverging ferruginous stripes traversing the black area longitudinally and dividing it into three subequal parts; the mesopleura with a large black spot somewhat anteriorly on their lower one-half (in some of the Ecuadoran specimens even more extensively darkened).

LEGS: As described for typical *pallida*.

WINGS: As described for typical *pallida*. Number of hamuli on each hind wing usually five, sometimes six. Of 14 wings available for examination 12 had five hamuli and two had six hamuli, an average of 5.14.

ABDOMEN: As described for typical *pallida* except that in the limited number of specimens available for study there is no instance of so intense a darkening of certain of the abdominal segments as was occasionally observed in exceptional specimens of typical *pallida*; the more apically located tergites, however, sometimes reddish brown rather than ferruginous.

MEASUREMENTS: Length 4.5 to 6 mm.; width of thorax 1.75 to 2 mm.; length of forewing, including tegula, 6.5 to 6.75 mm.

QUEEN

Unknown.

MALE

Unknown.

TYPE MATERIAL

This form was described from Porto Bello, Panama.

DISCUSSION

Cockerell (1917, p. 127), has pointed out the curious superficial resemblance of *ferricauda* to the structurally different *dorsalis* Smith (*ziegleri* Friese). The markings on the thorax are a virtual duplication of those of *dorsalis*, and the head, too, in its coloration offers a close approximation to the condition in that insect. However, even the lower half of the genal area is in *dorsalis* black as is the

malar space, while the sides of the face in *dorsalis* are yellow up to the level of, or slightly beyond, the base of the yellow clypeus, and frequently on the clypeus itself there are two subparallel, dark lines that are not found in *ferricauda*. The hind tibiae are wholly ferruginous in *ferricauda*, blackened at the apex as are their metatarsi in *dorsalis*. In its facial appearance *ferricauda* is also much like *williana*.

There is a very close resemblance, too, between the thoracic markings of *ferricauda* and of *chanchamayoensis*, but the head of *chanchamayoensis* usually accords in coloration with that of typical *pallida*.

Rau (1933, p. 38) throws light on the floral visits and other habits of *ferricauda* as observed by him at Barro Colorado Island, Canal Zone: "Dozens of these bees came to the brilliant red flowers of *Hibiscus rosa sinensis*. They did not go to the pistil, which extended far beyond the petals, but went down to the nectaries; hence they must have been in quest of nectar and not pollen. They also frequented the yellow flowers near the laboratory door. On one occasion they quickly carried away a large mass of animal excrement, which they transported in their pollen baskets on the hind legs."

At the same locality a bee of this variety was collected close to the trumpet-like entrance of the nest of *Trigona fulviventris* in the "Allee tree," but it was not actually observed making an attempt to enter the nest (Schwarz, 1934, p. 12).

DISTRIBUTION

Known from Panama and the Canal Zone, to which may now be added Ecuador. In the present collections the following localities are represented:

PANAMA: Chiriqui Grande, Apr. 15-16, 1924 (J. C. Bradley); Changuinola District, May 19, 1924 (F. R. Swift).

CANAL ZONE: Barro Colorado Island, July 18-Aug. 2, 1924 (N. Banks), Jan. 10, 1929 (C. H. Curran), Nov. 25, 1930 (H. F. Schwarz), Feb. 6, 1936 (F. E. Lutz); Ft. Sherman, July 3, 1924 (N. Banks); Río Pescado, April 15, 1945 (C. D. Michener).

ECUADOR: Bucay, 1000 feet, Oct. 4 and 10, 1922 (F. X. Williams); Naranjapata, 1850 feet, Dec., 1922 (F. X. Williams).

Trigona (Trigona) chanchamayoënsis, new species*Trigona Kohli*, SILVESTRI, 1902a, p. 25.*Trigona kohli*, SILVESTRI, 1902b, pp. 139-143, text figs. 9-10, pl. 1, fig. 18, pl. 3, fig. 45.*Trigona kohli*, BUTTEL-REEPEN, 1903a, pp. 133, 134, fig. 16.*Trigona Kohli*, SILVESTRI, 1903, pp. 187, 210-212.*Melipona Kohli*, DUCKE, 1916, opposite p. 28, pp. 127-128 (in part).*Trigona Kohli*, HEGH, 1922, p. 593.*Melipona kohli*, DUCKE, 1925, pp. 344, 415-416 (in part).*Melipona Kohli*, DUCKE, 1945, p. opposite 24, pp. 96-97 (in part).**WORKER**

DIAGNOSTIC CHARACTERS: Ferruginous, but with black areas on thorax and sometimes to a lesser extent on head (these darker areas often lacking in callows). Mandible five toothed. Length of malar space about

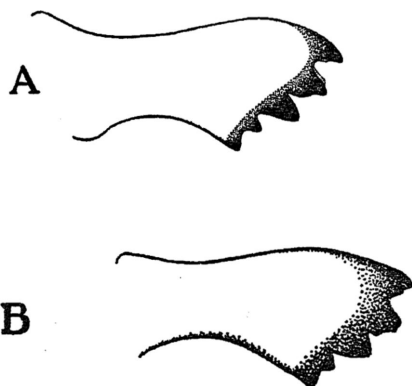


FIG. 40. *Trigona (Trigona) pallida* (Latreille) and *Trigona (Trigona) chanchamayoënsis*, new species, are in the worker hardly to be differentiated from each other structurally. The virtual identity of the mandible of *pallida* (A) with that of *chanchamayoënsis* (B) is indicated. Such light differences of dentition as may be noted are individual rather than specific. The mandibles are inverted in the figure.

equal to width of flagellum. Length of clypeus not quite one-half its greatest width. Labrum with two feeble prominences. Erect fulvous hairs on clypeus, supraclypeus, and scape. Hind tibiae with an inwardly placed angle posteriorly at the apex. The apex of the hind metatarsi posteriorly with an acute angulation in contrast with that of *pallida*. Wings

almost hyaline to diluted yellowish gray, subtransparent.

HEAD: As in typical *pallida*, almost completely bright unstained ferruginous to honey colored and structurally also like the head of that species. The facial quadrangle moderately wide, the distance between the compound eyes at the level just below the anterior ocellus being a little less (in the proportion of about 9 to 10) than the distance from the anterior ocellus to the apex of the clypeus. The compound eyes slightly convergent below, the distance that separates them at their level of greatest approximation (below) being about four-fifths of their divergence at the level just below the anterior ocellus. The clypeus and supraclypeus raised slightly above the sides of the face, of even surface and without a median fossa. The length of the clypeus not quite one-half its greatest width measured from one anterolateral extremity to the other; each anterolateral extremity of the clypeus separated from the nearest compound eye by less than one-half the width of the flagellum. The labrum with two more or less distinct tubercles. The mandibles armed with five teeth, the two innermost small (fig. 40B). The malar space, measured from the lower extremity of the eye to the middle of the base of the mandible, approximates the width of the flagellum. The distance between the lateral ocelli about equal to that separating each lateral ocellus from the nearest compound eye. The carina behind the ocelli low, blunt, and ill defined. Clypeus, front, vertex, and sides of face rather densely covered with silvery gray appressed microscopic hairs; the upper two-thirds of the genal area silvery gray pruinose (or viewed from certain angles yellowish). All the erect hairs of the head fulvous, those on the clypeus and supraclypeus long, more or less comparable in length with the hairs on the inner lateral surface of the scape and about as conspicuous as the hairs of the front. The hairs of the vertex, lower one-third of genal area, and inferior margin of mandibles longer. The head, completely or almost completely ferruginous to honey colored, may have two or three cloudy dots above the summit of the compound eye that are sometimes coalescent (these darker maculations are especially prevalent, among the specimens before me, in those collected

in the Colony of the Perené, Peru, and in Puyo, Oriente, Ecuador). As in *pallida*, the apex of the scape posteriorly is sometimes darkened and the flagellum above tends to be blackish except for sometimes the apical joint; teeth along apex of mandible darkened.

THORAX: Mesonotum differs from that of typical *pallida* in being black in varying degrees. Usually the entire mesonotum is black

of the mesonotum being wholly black. All three conditions may be represented in a series from a single locality. In addition, there is also sometimes a circular black maculation placed somewhat anteriorly at the lower extremity of the mesopleura (it occurs in the holotype). The prothorax long and collar-like, covered densely with silvery gray microscopic hairs; its length notably greater

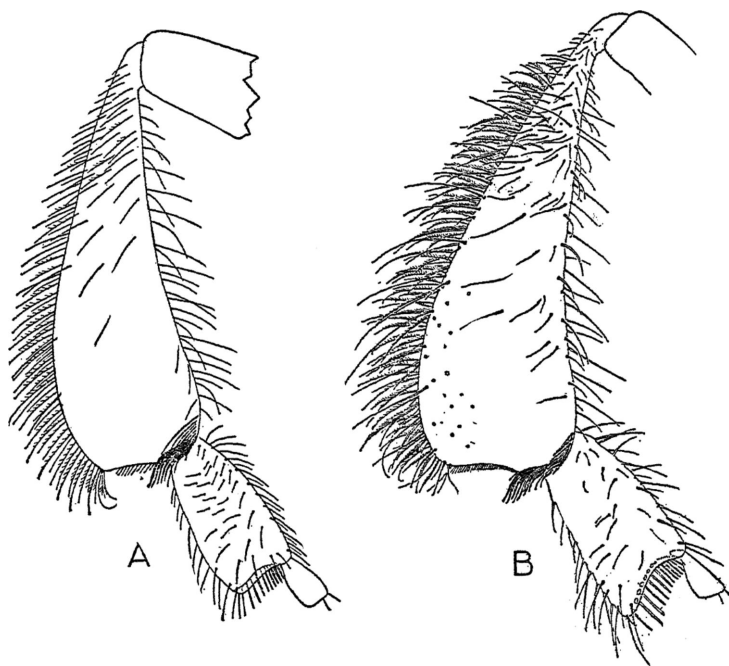


FIG. 41. Hind tibia and metatarsus of the worker of (A) *Trigona* (*Trigona*) *pallida* (Latreille), compared with those of (B) *Trigona* (*Trigona*) *chanchamayoënsis*, new species. The main structural difference is in the metatarsus. Drawings by Elena Feld (A), and Alice Gray (B).

except for narrow ferruginous lateral and hind margins (holotype), and sometimes two exceedingly narrow and posteriorly diverging ferruginous stripes that divide the black area approximately into thirds. More rarely, the central black area ordinarily bounded by these stripes is entirely ferruginous, with the result that only a long cuneiform spot on each side of the mesonotum is black. Finally there is the condition, intermediate between these two extremes, in which the median one-third of the mesonotum is more or less black anteriorly but red or red mottled with black posteriorly, each flanking outer one-third

than that of the scutellum. The mesonotum, scutellum, pleura, and sides of propodeum of somewhat subdued sheen due to the presence of silvery gray tomentum in addition to the erect simple hairs, which over the dorsal area and upper part of the mesopleura are fulvous but tend sometimes to become silvery gray towards the lower one-half of the mesopleura and the under side of the thorax; the erect hairs interspersed among the tomentum on the sides of the propodeum also mostly silvery gray. The relative length of the hairs of the thorax indicated in the description of the worker of the subgenus *Trigona*.

LEGS: Of a bright ferruginous. The hind tibiae (fig. 41B) clavate in outline, wider at the apex than at the base, their anterior lateral contour barely emarginate to straight, their posterior lateral contour strongly convex; their apex with an inconspicuous angle anteriorly that bears the tibial comb; beyond this angle there is a slight bulge in the apical contour followed by a shallow emargination that results in a somewhat inwardly placed angle where this emargination encounters the posterior contour of the joint. The outer face of the hind tibiae approximating a flattened condition on its basal three-fifths, particularly posteriorly, and lightly depressed on its apical two-fifths. The flattened area margining the under side of the hind tibiae posteriorly about one-third the width of the tibiae towards the apex. The hind metatarsi (fig. 41B) are more than one-half as wide at the apex as the hind tibiae, and are especially to be differentiated from the hind metatarsi of *pallida* by the sharply acute angulation of their apex posteriorly; the contrast between the rather wide apex and the narrowed base gives these metatarsi a somewhat subtriangular appearance. The hairs of the legs more or less fulvous except for the dense fringe of very microscopic whitish hairs usually traceable on the under side of the femora, the silvery gray plumose hairs on the outer face of the middle tibiae and adjoining basal region of the middle metatarsi, especially posteriorly, and the likewise silvery gray short but stubby hairs on the raised portion of the inner face of the hind tibiae and adjacent apical region of the under side of the hind femora. The suboval bristleless patch at the base of the under side of the hind metatarsi silvery gray to whitish sericeous but, when moistened, often gives the impression of being concolorous with the fulvous chitin. The relative length of the hairs and their distribution as indicated in the description of the worker of the subgenus *Trigona*.

WINGS: Of a uniform, almost hyaline to diluted yellowish gray stain, subtransparent; the median cell not darker than the other cells. The venation and stigma more or less ferruginous; the tegulae usually a slightly paler ferruginous. The transverse cubital veins are barely or not at all traceable. The

first discoidal cell about three-fourths the length of the marginal cell. Number of hamuli per lower wing usually five, rarely six. Of 128 wings examined 115 had five hamuli and 13 had six hamuli, an average of 5.10.

ABDOMEN: As a rule wholly or predominantly ferruginous to honey colored, but sometimes the segments, particularly those towards the apex, are largely or entirely black; somewhat narrower than the thorax; the tergites rather fully exposed instead of telescoped, tergites 5 and 6 tending to be vertical in position. The hairs on the tergites fulvous to pale, short, and relatively few. The appressed hairs along the apex of tergite 2 so inconspicuous as to be easily overlooked and those in the corresponding part of tergite 3 barely more in evidence. Tergite 4 with rather short erect hairs; tergites 5 and 6 with erect hairs that are rather longer. The tufts of fulvous to pale hairs at the middle of the apex of the several sternites are supplemented at each side of sternites 3 to 5 by glistening, dense, silvery gray sericeous patches.

MEASUREMENTS: Length 4.5 to 6 mm.; width of thorax 1.75 to 2 mm.; length of forewing, including tegula, about 6.75 mm.

QUEEN (GRAVID)¹

HEAD: A trifle wider than the mesonotum, but not nearly so wide as the distance between the outer rim of one of the tegulae and the outer rim of the other. The facial quad-angle wide, the distance between the compound eyes at the level below the middle ocellus about equal to the distance that separates the middle ocellus from the apical margin of the clypeus. The eyes very slightly convergent below, barely shorter and a little narrower than those of the worker. Eyes devoid of hairs. The clypeus gently arched; raised, like the supraclypeus, a little above the level of the sides of the face and of smooth surface. The width of the clypeus, measured from one apico-lateral extremity to the other, about twice its length. The labrum rather strongly bituberculate. The dentition of the mandibles obscured by intervening septa of chitin. The length of the malar space a little greater than the width of the flagellum, about

¹ Description based on a single specimen from La Merced, Valle de Chanchamayo, Peru.

one-sixth as long as the eye. The ocelli small and remote from the eye, the distance from the summit of the eye to the nearest lateral ocellus being about one and one-half times that separating each lateral ocellus from the other lateral ocellus. The carina behind the ocelli very feeble. The entire head shiny, little concealed by the exceedingly microscopic silvery gray hairs that cover all areas except the lower extremity of the genal area. Long fulvous hairs fringing the lower edge of the mandibles, these hairs being rather longer than the mandible is wide at the base. Similar long hairs sprouting forth from the labrum and a few also on the vertex, but the head otherwise devoid of conspicuous hairs. The scape with very fine and very short, pale, erect hairs. Ferruginous coloration barely cloudy here and there or faintly mottled, but only the upper side of the flagellum, the eyes, and the apex of the mandible definitely dark (probably there is some individual variation, as in the worker, in the coloration of the queen). The flagellum about twice the length of the scape and about of the same width.

THORAX: Shiny, especially on the mesonotum, ferruginous except for the brownish mesonotum edged laterally with ferruginous, and a dark spot anteriorly on the lower half of the mesopleuron. Width of thorax greater than that of the worker, the mesonotum of the queen measured along the base being about as 10 is to 7 compared with that of the worker, and virtually as wide as the combined mesonotum and scutellum are long. The mesonotum (except at the sides) and the pleura (except below) devoid of erect hairs, being covered with short silvery gray appressed hairs; the scutellum, however, with conspicuous fulvous hairs, some of which are about as long as the scutellum itself.

LEGS: Rather uniformly ferruginous. The hind tibiae about as long as the hind trochanters plus the hind femora, clavate to triangular in contour, wider apically than basally, their apex feebly rounded anteriorly, and with an obtuse angle posteriorly. The hind metatarsi about three-fifths as wide as the hind tibiae at the apex, rather parallel sided and briefly convergent at the base, in these respects like the hind metatarsi of the queen of *pallida* but differing from the latter in having a sharply acute angulation at the

apex posteriorly. The length of the hind metatarsi a little shorter than that of the combined small tarsal joints, the inner face rather uniformly covered with soft yellowish golden hairs of rather even length; fulvous bristles projecting beyond apex of joint. The brushes on the inner face of the fore and middle metatarsi yellowish golden. The other hairs of the leg also largely yellowish (except the hairs on the under side of the trochanters and the under side of the femora, which are more silvery gray). The femora are moderately hairy on their outer (anterior) and particularly under side, more glabrous on their inner (posterior) face. The hairs on the outer face of all the tibiae (including the hind pair) relatively dense and rather more erect than in the single available queen of *pallida*. Though they tend to be progressively longer from the fore tibiae to the hind tibiae, the contrast in length between those on the outer face of the fore tibiae and those on the outer face of the middle tibiae is not so marked as in the worker, and the plumose hairs that are present on the outer face of the middle tibiae of that caste are absent in the corresponding area of the queen. The hairs are longer posteriorly than anteriorly on all of the tibiae, and this applies also to the posterior lateral fringes on the several metatarsi. The fringe along the posterior lateral rim of the hind tibiae without admixture of plumose hairs.

WINGS: Badly mutilated in the only available specimen, completely lacking beyond the stigma. Surviving basal portion of wing almost hyaline to diluted yellowish gray. Hamuli destroyed. The tegulae of a slightly paler ferruginous stain than most of the venation of the remaining fragment of the wing.

ABDOMEN: Ferruginous, rather shiny. Tergites 1 and 2 virtually glabrous. The hairs on tergites 3 to 6 fine and soft, silvery gray to, in some lights, fulvous, short, and although increasing in length from base to apex on each of these tergites, nevertheless not notably longer from tergite to tergite when hairs that are correspondingly placed are compared. No clearly traceable punctuation of the tergites. Erect fulvous to silvery gray hairs on the apical half of the successive sternites.

MEASUREMENTS: Length about 9.5 mm.

(of which the abdomen occupies about 6.5); width of thorax about 2.75 mm.; wing measurement not obtainable because of fragmentation.

MALE

Structurally very close to *pallida* but the genitalia different (compare fig. 39A with fig. 42A).

HEAD: Ferruginous or at least predominantly ferruginous (in one of the paratypes the head, in the main ferruginous, has a dark stripe along the inner orbit of each of the compound eyes and a down-pointing triangle of brownish black; its base coextensive with the ocelli, its apex extending close to the top of the supraclypeal area, recalling a maculation frequent in *dallatorreana*; this paratype was collected between Huacapistana and San Ramon, Peru). Facial quadrangle much narrower than in the worker. The distance from one eye to the other at their level of closest approximation is nearly three-fifths the length of the eye, whereas in the worker the shortest distance between the eyes is about five-sixths of the length of the eye. The clypeus and supraclypeus barely more prominent than the sides of the face; the apico-lateral extremities of the clypeus approximating the rectangular and grazing or almost grazing the rim of the eye; the length of the clypeus about two-thirds its greatest width. The labrum much less distinctly bituberculate than is the case in the worker, the very feeble eminences barely discernible. The mandible rather thumb shaped, bluntly pointed at the apex, and edentate. The malar space virtually obsolete, the inner angle at the base of the mandible grazing the rim of the eye. The distance between the lateral ocelli a little greater than that between each lateral ocellus and the nearest compound eye. The carina behind the ocelli low, blunt, and ill defined. The head about as hirsute as, to a little more hirsute than, the moderately hirsute head of the conspecific worker. The dense appressed microscopic hairs on the clypeus, sides of face, front, vertex, and genal area (densely covering all but the lower extremity of this area) silvery gray. The erect hairs silvery gray to fulvous; those of the clypeus long and rather evenly distributed, notably longer than the inconspicuous fine

hairs on the scape and approximating the length of the erect hairs of the front; most of the hairs on the lower extremity of genal area, some of those along lower margin of mandibles, and especially those on the vertex longer than the clypeal hairs. The flagellum somewhat darkened above but ferruginous below as is the entire scape.

THORAX: With the pronotum ferruginous. The mesonotum either with a large black cuneiform maculation on each side of an otherwise ferruginous surface or, instead, black throughout except for narrow ferruginous side and hind margins (callows?), showing the same variability in these respects as does the worker. The axillae and scutellum wholly ferruginous. The mesopleura pure ferruginous to cloudy ferruginous on their upper half and blackish on their lower half. The metapleura and propodeum mainly ferruginous, but the hairless middle region of the propodeum feebly brownish. The hairs of the mesonotum very short, for the most part appressed or semi-appressed and silvery gray to slightly fulvous; the slightly longer and more erect hairs of the mesopleura likewise silvery gray. The long erect hairs of the scutellum, which are fulvous to silvery gray, completely dwarf the other hairs of the thorax and are intermixed with silvery gray tomentum, which is especially dense also in the region at each side of the hairless middle region of the propodeum.

LEGS: Bright ferruginous. The hind tibiae narrow, almost straight (a little convex towards the apex) along their anterior lateral contour, somewhat convex along their posterior lateral contour, the posterior part of the outer face rather flattened and, towards the apex especially, even somewhat concave; the contour of the apex of these tibiae somewhat irregularly rounded; their greatest width (near the apex) about two-thirds that of the conspecific worker at the corresponding level. The hind metatarsi only a shade narrower than the associated tibiae, being fully four-fifths as wide, the posterior apical extremity of these metatarsi virtually subrectangular to very slightly acute. The hairs predominantly more or less fulvous, those on the under side of the trochanters, the very microscopic fringes along the under side of the femora, the microscopic but stubby hairs down the raised

area on the under side of the hind tibiae and the adjacent region at the apex of the under side of the hind femora, and the small area of appressed sericeous hairs at the base of the under side of the hind metatarsi all tending to be more or less whitish to silvery gray, although the differentiation from the more fulvous hairs is often very slight. The simple hairs on the outer face of the fore and even of the middle tibiae few and exceedingly short, conspicuously shorter than the hairs on the under side of the middle tibiae and along the posterior lateral margin of the fore

uniform almost hyaline to diluted yellowish gray stain, subtransparent; the median cell not darker than the other cells. Number of hamuli per lower wing, in the three males available, ranges from five to six. Of the six wings, five have five hamuli and one has six hamuli, an average of 5.16.

ABDOMEN: Ferruginous and approximating the thorax in width. Tergites 1 and 2 bare, and tergite 3 with only a few exceedingly short, sparse, inconspicuous hairs, more especially in the apical region; tergites 4 to 6 with erect hairs of intermediate length and in

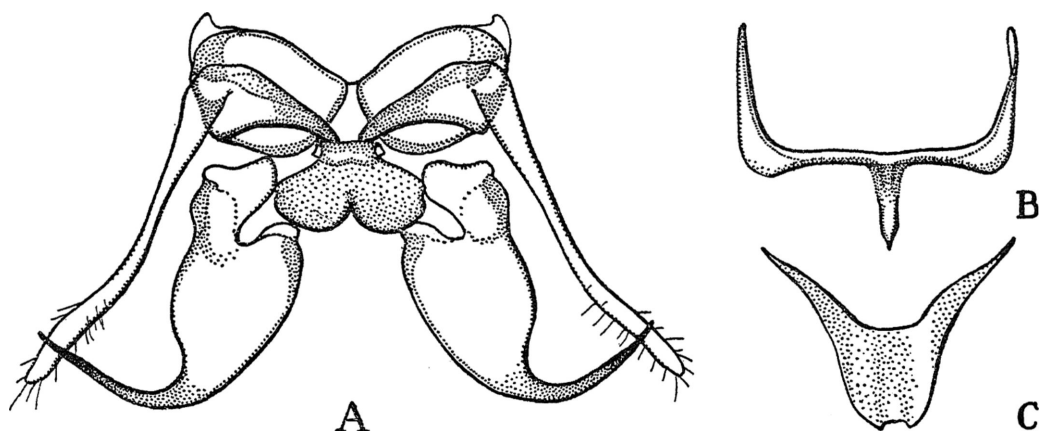


FIG. 42. Abdominal parts of male of *Trigona* (*Trigona*) *chanchamayoensis*, new species. A. Genitalia (chitinized parts only). B. Sternite 6. C. Sternite 7. All based on specimen collected between Huacapistana and San Ramon, Peru. Drawings by Shirley H. Risser.

and middle tibiae and of all the metatarsi; and in general the distribution and the relative length of the hairs accord approximately with the specifications set down in the generalized description of the male of *Trigona*. The plumose hairs (if the limited number of specimens before me are representative in this respect) are much more abundant on the outer face and along the posterior lateral contour of the middle and especially the hind tibiae than is the case in the few specimens before me of the male of the closely related *pallida*. The simple hairs in the fringe along the posterior lateral contour of the hind tibiae longer than the plumose hairs of the same fringe, their length being about one-half the width of the hind tibiae, but they tend to be shorter than the simple hairs fringing the hind metatarsi posteriorly.

WINGS: Like those of the worker, of a

the main fulvous; tergite 7 fringed apically with moderately long incurved hairs. The sericeous hairs of the sternites silvery white. For the structure of the sternites and the genitalia, see figure 42.

MEASUREMENTS: Length about 5.25 mm.; width of thorax about 2 mm.; length of forewing, including tegula, 6.5 to 6.75 mm.

TYPE MATERIAL

Holotype (worker) collected from a nest at San Ramon, and queen from La Merced (both localities in Valle de Chanchamayo, Peru), as well as paratypes, in the American Museum of Natural History; paratypes also in the Academy of Natural Sciences of Philadelphia, at Cornell University, in the United States National Museum, and in the collection of Dr. J. Bequaert.

DISCUSSION

Friese (1900a, p. 387) described *kohli* (here considered a synonym of *pallida*) very briefly, giving the impression by his employment of the word "ferruginea" without qualification that this species is devoid of black markings. Friese's type material included specimens from Peru, Colombia, French Guiana, Dutch Guiana, and Brazil. Silvestri (1902b, p. 139) designated as *kohli* specimens from Cuyabá and Corumbá, both in the western part of the State of Matto Grosso and neither a great distance from the Bolivian boundary. The description of Silvestri departs, however, from the description of Friese in that Silvestri particularly specified that the mesonotum is black ("mesonoto nigro"). Ducke (1902b, p. 303) described *kohli* from the State of Pará as "wholly rust-yellow," so that it is to be presumed that his material from that state did not include specimens with blackened mesonotum. Later (1916, p. 127; 1925, p. 415; 1945, p. 96) Ducke made his description of *kohli* broad enough, however, to include specimens that have the mesonotum exclusively ferruginous and likewise those in which the mesonotum is in part black. Ducke's conclusions were based not merely on specimens from Brazil, especially the State of Pará, but included also Peruvian specimens and the records from western Matto Grosso of Silvestri. It would be interesting to know whether the insect with black mesonotum was represented in Ducke's material by specimens other than those Ducke had from Peru supplemented by Silvestri's records.

The form with dark mesonotum I have here separated as a distinct species, *chanchamayoënsis*, because it is different from *pallida* not only in its coloration but also in its structure. The male of *chanchamayoënsis* has genitalia distinct from those of *pallida*, and the worker, too, tends to separate itself structurally through the decidedly acute angulation at the apex posteriorly of its hind metatarsi and other characters. Before me are specimens of this insect from Bolivia that Friese designated as *Trigona kohli tarataënsis*. However, I have been unable to find any published record of *tarataënsis* and am forced to conclude it is a manuscript name.

It should be mentioned that the closely related *ferricauda* from Panama shares with

typical *chanchamayoënsis* the black mesonotum and has, in addition, much black on the head, but *ferricauda*, if one may judge from the only caste known (the worker), aligns itself structurally with *pallida* and is here made a variety of that species.

The wing length of *chanchamayoënsis* slightly exceeds that of typical *pallida*.

The close affiliation of *chanchamayoënsis* to *pallida* is further emphasized by the fact that it shares with *pallida* a partiality for the nests of termites as the seat of its colonies. Thus at La Merced, Peru, W. Weyrauch found a termite nest 80 cm. in length and 55 cm. in breadth that was plastered against the wall of a house immediately under the projecting part of the roof. In this nest was a colony (or more likely daughter colonies) of the bee here considered. Dr. Weyrauch in a letter to me described the nest entrance as 1 cm. high and 4 cm. wide. The entrance was extended inward in the form of a tube that subdivided into three passageways. These passageways led to five large chambers that lay, completely separated from one another, in the hard mass of the old termite nest. The five chambers were almost completely occupied by brood combs arranged in regular fashion one above the other, very densely crowded. Some of the combs were in places joined with the neighboring combs, or there were forkings of a single comb into a main comb and a daughter comb branching out from it diagonally below. The combs containing eggs and honey were, according to Weyrauch's observations, blackish brown.

The mass of combs of each of the five chambers was enveloped by a compact thick black layer of resin and of remnants of the termite nest. This wall was in each case so hard that it was difficult to break it. The wall was 3 to 4 mm. in width and furnished in each of the five instances a barrier of protection against the incursions of ants that had established themselves in the greater part of the termite structure. A slight space separated each enveloping wall from the brood combs that it enclosed, and there was a space of corresponding width separating the outer side of the wall from the adjacent part of the termite nest. On its inner side the wall was attached to the enclosed combs by tiny pillars, and similar structural elements ex-

tended from its outer surface to the contiguous part of the termite nest.

Only in two of the five chambers was there evidence of provision jars, and in these two cases the jars, of black wax, were placed above and below the mass of brood combs although separated from the latter. The jars were, according to Weyrauch, very variable in form and size notwithstanding the fact that for the most part they were small. Some of his measurements were as follows: 8 mm. by 12 mm., 7 mm. by 9 mm., 4 mm. by 8 mm., 3 mm. by 5 mm.

The five chambers containing brood were, as already indicated, widely separated from one another and gave Weyrauch the impression that they functioned as independent entities. No chamber had more than six combs, and the poorest equipped of all had only three. The dimensions of the several combs, as recorded by Weyrauch, were as follows:

	Chamber 1	Chamber 2	Chamber 3	Chamber 4	Chamber 5
Comb 1	3 by 4 cm.	4 by 5 cm.	3 by 4 cm.	5 by 5 cm.	5 by 6 cm.
Comb 2	5 by 6 cm.	6 by 6 cm.	5 by 6 cm.	5 by 6 cm.	5 by 7 cm.
Comb 3	7 by 11 cm.	6 by 9 cm.	7 by 13 cm.	6 by 7 cm.	6 by 7 cm.
Comb 4	7 by 11 cm.	9 by 10 cm.	5 by 12 cm.	7 by 8 cm.	
Comb 5	7 by 10 cm.	8 by 9 cm.	5 by 12 cm.	4 by 6 cm.	
Comb 6			3 by 11 cm.		

The combs were united with one another through pillars of fragile brown material (wax and resin), and in some instances these supports extended through three or four combs.

Although the nest consisted of five separated chambers, only a single queen (and that one physogastric) was observed. Furthermore there was no evidence of royal cells. The absence of both virgin queens and of cradles of queens derives additional interest from the fact that of the more than 850 individual bees that Weyrauch sent me from this bee community all were workers. There was not a single male. (See p. 61.)

Altogether this account of Weyrauch has one completely puzzled. The well-separated brood chambers suggest at least semi-independent activities of daughter colonies. The single queen, the absence of provision containers in three of the units, and the common entrance to the nest raise, on the other hand,

a picture of interdependence among the several units.

Another nest of *chanchamayoënsis* that was ensconced in a termite structure was observed by Weyrauch at San Ramon, also a locality in the Valle de Chanchamayo, Peru. In this area, too, individuals of this species were seen lapping honey from the fragments of a discarded comb.

It was *chanchamayoënsis* in my estimation that Silvestri (1902b, pp. 139-143; 1903, pp. 210-212) mistakenly interpreted as the very closely related *kohli* Friese, itself a synonym of *pallida* Latreille. Silvestri described the nest, which, as were the nests above referred to, was within a termite structure, in this instance an exposed termite structure [that of *Nasutitermes* (N.) *breviocularatus* according to Holmgren, 1910] on the branch of a tree. In fact, Silvestri observed nests of this bee thus associated with this termite not once but on four different occasions, which, taken in

connection with Weyrauch's records, would seem to indicate that *chanchamayoënsis* is very definitely termitophilous. The bees' nest, Silvestri indicated, had a major axis of 48 cm. and a minor axis of 28 cm. and was oval in shape. The extent to which the bees had encroached upon the domicile of the host species is evidenced by the fact that the termite structure itself, including the *Trigona* nest in its interior, was not substantially larger than the bees' nest considered by itself, being only 65 cm. by 40 cm. The bees' nest was walled off from the enclosing termite nest by a very hard black propolis. The combs were horizontally arranged, and in the lower part of the nest especially were the honey and pollen pots. On the periphery of the combs or more often attached to the wall of the nest were here and there royal cells of nearly twice the size of those of the worker. The entrance of the nest presented nothing unusual, consisting of a hole which communi-

cated with a gallery completely enclosed by hard propolis. Silvestri affirmed that it is absolutely certain that the *Trigona* invades the dwelling of the termite and not the reverse.

Silvestri paid tribute to the aggressiveness of this species when molested, indicating that it bites furiously "but perhaps with less violence than *Trigona ruficrus*."

The same author indicated that the honey is somewhat dense, clear, and of dark color resembling that of Marsala wine, and rather sweet.

To this bee has been given the popular name "cupira," which was adopted as the scientific name for a bee of very different structure, namely, a member of the subgenus *Paratamona*. Both Smith's *cupira* and *chanchamayoënsis*, though very different in their plastic characters, have this in common: they both tend to occupy the nests of termites, which in the Brazilian vernacular are known as "cupi." The derivation of "cupira" from "cupi" (Silvestri, 1902b, p. 143; 1903, p. 212) seems far more plausible than does its alleged derivation from "curupira," denoting fiend of the forest (Smith, 1863a, p. 503). The name "cupira" is also applied to *Trigona (Trigona) pallida*.

DISTRIBUTION

So far as the rather extensive material of *pallida* and *chanchamayoënsis* before me may justify a conclusion, the territory of *pallida* includes Central America, the northern tier of South American states bordering the Caribbean (or most of them), as well as localities in the northern part, at least, of Brazil. On the other hand, *chanchamayoënsis* is particularly representative of the west coast states of South America and of some, at least, of the adjacent areas of Brazil. The localities where *chanchamayoënsis* was taken are listed herewith:

BOLIVIA: Tarata, 1900 (Priewasse); Mapiri, 1900 (these specimens were designated *Tr. kohli tarataënsis* by Friese); Rurrenabaque, Río Beni, Nov. (W. M. Mann).

PERU: Yurimaguas, March 27, 1920 (H. Parish); Huacapistana to San Ramon, male, June 3, 1920 (Cornell Univ. Exped.); Hacienda No. 2, Colony of the Perené, June 23, 1920 (Cornell Univ. Exped.); El Campamento, Colony of the Perené, male as well as workers, June 18-21, 1920 (Cornell Univ. Exped.); Hacienda San Juan,

Colony of the Perené, June 23, 1920 (Cornell Univ. Exped.); Puerto Bermudez, Río Pichis, July 18-19, 1920 (Cornell Univ. Exped.); lower Río Pachitea, July 23, 1920 (Cornell Univ. Exped.); La Merced, Valle de Chanchamayo, 800 meters, March 2, 1940, No. 34, nest in termite nest, including queen (W. Weyrauch); San Ramon, Valle de Chanchamayo, 800 meters, Feb. 5, 1940, No. 7, nest in termite nest, including males (W. Weyrauch), and Feb. 25, 1940, lapping honey from the fragments of a discarded comb (W. Weyrauch).

ECUADOR: Guayaquil, Nov., 1902 (Buchwald); Abitagua, Oriente, 1200 meters (W. Clarke-MacIntyre); Tena, March 16, 1923 (F. X. Williams); Puyo, Oriente, Dec. 5, 1938 (F. M. Brown); Baños, Nov. 20, 1938 (F. M. Brown).

BRAZIL: State of Matto Grosso (western part): Coxipó, 1900 (F. Silvestri); Corumbá, April (H. H. Smith); Urucúm (Corumbá), Dec. 23-29, 1919 (Cornell Univ. Exped.).

Trigona (Trigona) amapana, new species

WORKER

Unknown.

QUEEN

Unknown.

MALE

HEAD: As is the rest of the body, bright ferruginous except for the vertex and the area about the outer orbit of the eye, which tend to be cloudy. The facial quadrangle very narrow. The distance from one eye to the other at the level of closest approximation is only a little more than one-half the length of the eye. The clypeus and supraclypeus barely more prominent than the sides of the face; the apico-lateral extremities of the clypeus rectangular, grazing or almost grazing the rim of the eye; the length of the clypeus about two-thirds its greatest width. The labrum depressed along its basal middle, slightly swollen at each side. The mandibles shaped somewhat like a thumb, bluntly pointed at the apex (rather than inwardly receding), and edentate. The malar space virtually obsolete, the inner angle at the base of the mandible almost in contact with the rim of the eye. The ocelli large, the lateral ones relatively far removed from each other and correspondingly close to the nearest compound eye, from which each is separated

by only about its own diameter. The carina behind the lateral ocelli low, blunt, and ill defined. The head moderately hirsute. The dense, appressed, microscopic hairs on the clypeus, sides of face, front, vertex, and genal area (densely covering all but the lower extremity of this area) silvery gray. Silvery gray, too, are the fine erect hairs on the clypeus, which greatly exceed in length the dwarfed, fine, silvery gray hairs of the scape and are longer, too, if anything, than the hairs of the front. The hairs on the vertex usually distinctly fulvous and much longer, and some of the pale hairs fringing the mandibles below and the erect hairs towards the lower extremity of genal area also tend to be longer than the hairs of the clypeus. The scape pale ferruginous, with a dark spot at the apex posteriorly; the dark upper side and the ferruginous under side of the flagellum strongly contrasted.

THORAX: Ferruginous, but of deeper tinge (sometimes even brownish) on the mesonotum compared with the paler mesopleura and scutellum. The hairs silvery gray, very short, and in large part appressed and inconspicuous on the mesonotum; rather short, semi-appressed, in part tomentose, and more pronouncedly silvery gray on the mesopleura; much longer, erect, and somewhat brownish yellow on the scutellum, which is also to some extent tomentose. The area at each side of the shiny bare middle portion of the propodeum silvery gray tomentose with rather long, silvery gray, erect hairs interspersed.

LEGS: Ferruginous. The hind tibiae very narrow, almost straight (a little convex towards the apex) along their anterior lateral contour, very feebly convex along their posterior lateral contour, the width at the apex only a little greater than the width at the base, the posterior part of the outer face flattened towards the apex; the contour of the apex of these tibiae rounded anteriorly, subangular posteriorly. The hind metatarsi only a shade narrower than the associated tibiae, being fully four-fifths their width, the posterior apical extremity of these metatarsi subrectangular to rounded. The hairs predominantly more or less fulvous, those on the coxae, under side of the trochanters, the very microscopic fringes on the under side of the

femora, the microscopic but stubby hairs down the raised area on the under side of the hind tibiae and the adjacent region at the apex of the under side of the hind femora, and the small and feebly differentiated area of appressed hairs at the base of the under side of the hind metatarsi, all tending to be more or less whitish to silvery gray, although the differentiation from the more fulvous hairs is often far from distinct. The hairs on the posterior face of the hind coxae very notably longer than those on the anterior face of this joint and conspicuously longer, too, than the hairs on the under side of the fore, middle, and hind trochanters. The simple hairs on the outer face of the fore and even of the middle tibiae few and exceedingly short, conspicuously shorter than the hairs on the under side of the middle tibiae and along the posterior lateral margin of the fore and middle tibiae and of all the metatarsi. In general the distribution and the relative length of the hairs correspond approximately with the specifications in the generalized description of the male of subgenus *Trigona*. No, or virtually no, traceable plumose hairs on the outer face of the middle tibiae, and the hind tibiae posteriorly with a dense fringe of only exceedingly stunted tomentose hairs that are completely dwarfed by the rather short and sparse simple hairs (the length of these simple hairs approximating one-half the width of the joint) that occur along the anterior as well as the posterior lateral contours of these tibiae.

WINGS: Of a uniform, almost hyaline to diluted yellowish gray stain, subtransparent, the median cell not darker than the other cells; the venation and stigma brownish, the tegulae bright ferruginous. The surviving upper half of the first transverse cubital vein more clearly demarked than is the faded to obsolete second transverse cubital. The first discoidal cell about three-fourths as long as the marginal cell. The number of hamuli, in the four specimens before me, ranges from four to five with an average of 4.88.

ABDOMEN: Approximating the thorax in width, ferruginous, the apex of the several tergites sometimes more or less darkly banded. The hairs of the tergites very microscopic, sparse, and silvery gray (in the case of specimens with the apices darkened, the

hairs tend to be dark too) and on tergites 2 to 4 confined to the apex; tergite 1 devoid of hairs. The venter silvery gray sericeous. For the structure of the sternites and the genitalia, see figure 43.

MEASUREMENTS: Length 5 to 5.5 mm.; width of thorax about 1.75 mm.; length of forewing, including tegula, about 6 mm.

Ducke gave of the male of *kohli* seems to apply well to the present specimens. Unfortunately Ducke did not indicate whether he had also workers from Amapá. If workers were present and were structurally not to be separated from *kohli* (= *pallida*), then we have an instance like that of *pallida* and *chanchamayoënsis*, where the workers have

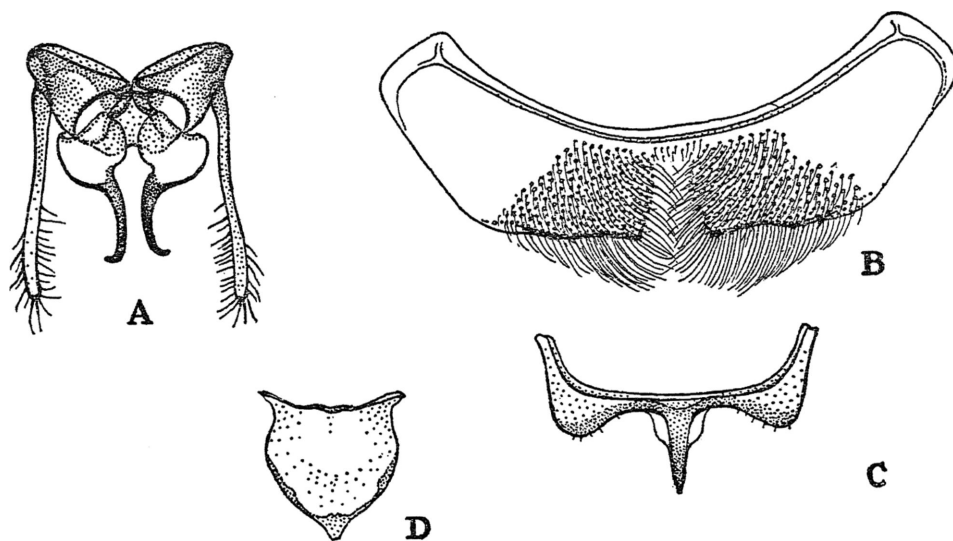


FIG. 43. Abdominal parts of male of *Trigona* (*Trigona*) *amapana*, new species. A. Genitalia (chitinized parts only). B. Sternite 5. C. Sternite 6. D. Sternite 7. All based on specimen from Amapá, State of Pará, Brazil. Drawings by Shirley H. Risser.

TYPE MATERIAL

The type material, from Amapá, State of Pará, Brazil, is in the American Museum of Natural History.

DISCUSSION

The four specimens on which this species is based were all collected by Ducke and were identified by Friese as *pallida*. Friese's conception of *pallida* ordinarily accords with what I have interpreted as *testacea*, and the present bees are very different from the male of that species. Almost certainly they are part of the same catch that Ducke himself (1916, p. 128; 1925, p. 416; 1945, p. 97) referred to *kohli*, a synonym of *pallida* as I interpret *pallida*. Ducke listed Amapá as a collecting site for *kohli*, and in no other part of Ducke's three papers is Amapá mentioned as a collecting site for any species other than *kohli*. Moreover, the brief description that

virtually the same plastic characters but the males are separable on the basis of their genitalia.

This raises a problem. Originally *pallida* was described from French Guiana on the basis of the worker only. Likewise *kohli*, though based on specimens from Peru, Colombia, French Guiana, Surinam, and Brazil, was described only from the worker. Yet the males from Amapá are different from males of other regions that I associate with workers of *pallida*, and both cannot, therefore, be *pallida*. Is the male from Amapá to be considered the valid *pallida* male, or should preference be given to what I have described as such? Or is it possible that perhaps neither qualifies? The male of *chanchamayoënsis*, for instance, does not accord in its genitalia with either the male of *amapana* or with the males I have designated *pallida*, yet the worker of *chanchamayoënsis* is structurally virtually the

same as that of *pallida*. In the present state of our knowledge and without wider collecting of males in association with workers that structurally resemble *pallida*, it is impossible to reach a definite conclusion. It is possible that some of the localities at least that are grouped under typical *pallida* on the basis of the worker should be assigned to *amapana*, but the presence of the male is needed to make possible a decision.

DISTRIBUTION

As yet known with certainty only from Amapá, State of Pará, Brazil, where specimens were collected by Ducke.

Trigona (Trigona) williana Friese

- Trigona williana* FRIESE, 1900a, p. 388.
Melipona williana, DUCKE, 1902a, p. 420.
Melipona (Trigona) williana, DUCKE, 1902b, pp. 290, 303-304.
Trigona williana, SCHULZ, 1904b, p. 821.
Trigona rhodoptera COCKERELL, 1912b, p. 49.
Melipona williana, DUCKE, 1916, opposite p. 28, pp. 125-126, pl. 6, fig. 19.
Trigona williana, COCKERELL, 1920c, pp. 462-463.
Trigona williana, COCKERELL, 1922, p. 8.
Trigona williana, LE COINTE, 1922, p. 383.
Trigona williana, COCKERELL, 1923a, p. 452.
Melipona williana, DUCKE, 1925, pp. 344, 354, 413-415, text fig. W, pl. 4, fig. 19.
Trigona (Trigona) williana, SCHWARZ, 1938, pp. 438, 443, 460-462, pl. 52, figs. C, D, pl. 53, figs. D, E.
Trigona (Trigona) williana, SCHWARZ, 1940, p. 5.
Trigona villana (sic), SOUKUP, 1943, p. 271.
Melipona williana, DUCKE, 1945, opposite p. 24, pp. 94-96, pl. 6, fig. 19.
Trigona williana, LE COINTE, 1945, p. 163.

WORKER

DIAGNOSTIC CHARACTERS: Mainly ferruginous but, especially on the head, with contrasting black areas, vertex, front, and sides of face being usually black. Mandible five toothed. Length of malar space about equal to width of flagellum. The clypeus, with a maximum width about twice as great as its length, is flat to very gently arched and of even surface, without a fossa and not foveate apically. The erect hairs fulvous on clypeus, supraclypeus, and scape. Facial quadrangle longer than wide. Hind tibiae with an inwardly placed angle posteriorly at the apex.

Wings long, extending far beyond abdomen, subtransparent, of rather strongly yellowish tinge. Considerably larger than *pallida* and *chanchamayoensis*.

HEAD (FIG. 37C): With its upper part darkened; in extreme cases the genal area (except for its ferruginous shiny lower one-third), the vertex, front, and sides of face are black, but often some or all of these parts are invaded or replaced by dark red; in contrast the clypeus, supraclypeus, labrum, and scape are conspicuously ferruginous against this darker setting. At its apex posteriorly the scape is blackish; the flagellum is dark above but more or less ferruginous below, with the apical joint usually wholly or partly ferruginous above as well as below. The mandibles sometimes ferruginous at the base but of a more intense red as the apex is approached and with black apical teeth. The facial quadrangle longer than wide, the distance between the compound eyes at the level just below the anterior ocellus less (in the proportion of about 9 to 11) than the distance from the anterior ocellus to the apex of the clypeus. The compound eyes only very slightly convergent below, the distance that separates them at their level of greatest approximation (below) being about as 5.5 is to 6 when compared with their divergence at the level just below the anterior ocellus. The clypeus and supraclypeus raised only slightly above the sides of the face; the clypeus rather flat to very gently arched, of even surface, without a fossa and not foveate apically. The length of the clypeus about one-half its greatest width measured from one anterolateral extremity to the other; each anterolateral extremity of the clypeus separated from the nearest compound eye by less than one-half the width of the flagellum. The labrum barely thickened to each side, the resulting elevations of surface almost negligibly slight and much less distinct than in *pallida* and *chanchamayoensis*. The mandibles armed with five teeth, the two innermost separated by a feeble emargination. The malar space, measured from the lower extremity of the eye to the middle of the base of the mandible, approximates the width of the flagellum, but the inner extremity of the malar space (near the inner angle of the base of the mandible) extremely short, eye and mandible being at

this point very narrowly separated. The distance between the lateral ocelli somewhat less than that separating each lateral ocellus from the nearest compound eye. The carina behind the ocelli low and blunt. The sides of the face, the front (less strongly), the genal area except for its shiny lower one-third, and the malar space silvery gray pruinose (frequently inclining to pale yellowish or olivaceous on the genal area); the clypeus with similar appressed silvery gray hairs but these sparser. The erect hairs fulvous on clypeus, supraclypeus, and scape, fulvous to darker on the front, almost invariably fulvous (rarely black) on the vertex, fulvous on the lower margin of the mandibles and on the lower one-third of the genal area. The hairs on the clypeus and supraclypeus somewhat comparable in length to those on the front, and those along the inner face of the scape likewise rather long, usually approximately as long as the scape is wide. The hairs of the vertex, lower one-third of genal area, labrum, and inferior margin of mandibles longer.

THORAX: Ferruginous with sometimes suffusion of darker red (in rare instances even blackish over the mesonotum). The mesonotum, scutellum, mesopleura, and sides of propodeum fairly densely covered with fulvous to reddish hairs in addition to the dense silvery gray tomentum, with resulting subdued shininess. The prothorax long and collar-like, densely covered with silvery gray, microscopic hairs, its length perceptibly greater than that of the scutellum. The relative length of the hairs of the thorax as indicated in the description of the subgenus *Trigona*.

LEGS: Ferruginous to deeper red, with the middle and hind metatarsi and the apex of the hind tibiae sometimes a little more intensely red than the other joints. The hind tibiae (fig. 38D) clavate in outline, wider at the apex than at the base, their anterior lateral contour very slightly emarginate, their posterior lateral contour strongly convex; their apex with an angle anteriorly that bears the tibial comb; beyond this angle there is a slight bulge in the apical contour followed by an emargination that results in a somewhat inwardly placed angle where this emargination encounters the posterior contour of the joint. The outer face of the hind tibiae

approximating a flattened condition on its basal three-fifths, especially posteriorly, and somewhat depressed on its apical two-fifths, especially posteriorly. The flattened area that constitutes the posterior part of the under side of the hind tibiae about two-fifths the width of the joint towards the apex. The hind metatarsi rather long, three-fifths the width of the hind tibiae at their widest, their apex posteriorly rather rectangular. The hairs of the leg largely fulvous to slightly reddish except for the dense fringe of very microscopic whitish hairs usually traceable on the under side of the femora, the pale plumose hairs on the outer face of the middle tibiae and adjacent area at the base of the middle metatarsi, the microscopic but stubby silvery gray hairs over the raised portion of the under side of the hind tibiae and over the contiguous area at the apex of the under side of the hind femora. The suboval bristleless patch at the base of the under side of the hind metatarsi silvery gray sericeous, but often the patch is glazed over with sticky matter and in such cases the hairs tend to blend with the fulvous coloration of the chitin. The relative length of the hairs and their distribution as indicated in the description of the worker of the subgenus *Trigona*.

WINGS: Long, extending far beyond the abdomen, subtransparent, of rather strongly yellowish tinge, with orange-colored venation and stigma. The tegulae concolorous with the venation or a little paler. The transverse cubital veins are virtually absent or traceable only with difficulty. Rest of venation rather distinct in both upper and lower wings but the marginal vein often with a tendency to thin out at the apical extremity. The first discoidal cell about three-fourths as long as the marginal. Number of hamuli on each lower wing usually five, rarely six, very exceptionally four or seven. Of 140 wings examined only one had as many as seven hamuli and only two as few as four hamuli; 115 had five hamuli and 22 had six hamuli, an average of 5.15 hamuli per wing.

ABDOMEN: With the color somewhat variable, rarely wholly ferruginous, usually more deeply red to cloudy blackish red or even black on some or most of the segments, particularly those towards the apex; somewhat narrower than the thorax; the tergites in

most cases rather fully exposed instead of telescoped, tergites 5 and 6 tending to be vertical in position. The hairs fulvous to sometimes slightly fuscous; those along the apex of tergite 2 so diminutive and appressed that they are detected only with difficulty; the sparse and short hairs along the apex and sometimes laterally on tergite 3 semi-erect; the hairs on tergites 4 to 6 longer, more abundant, and semi-erect to erect. A small aggregate of erect yellowish to reddish hairs at the middle of the apex of each of the successive sternites, supplemented in the case of sternites 3 to 5 by glistening, dense, silvery gray, sericeous lateral patches.

MEASUREMENTS: Length 6.5 to 9 mm., depending on the retraction of the segments of the abdomen (Ducke had specimens measuring up to 9.5 mm.); width of thorax 2.5 to 2.75 mm.; length of forewing, including tegula, 9 to 9.5 mm.

QUEEN

Unknown.

MALE

HEAD (FIG. 37D): With the upper part darkened as in the worker and, as in that caste, the clypeus, supraclypeus, scape, and labrum usually ferruginous (but in some cases entire head black); the mandibles reddish brown to black with a more or less distinct reddish stripe immediately behind the apex. Facial quadrangle narrower than that of the worker. The distance from one eye to the other at their level of maximum approximation (below) is about three-fifths of the length of the eye, whereas in the worker the shortest distance between the eyes is about five-sixths of the length of the eye. The clypeus and supraclypeus barely more prominent than the sides of the face; the apico-lateral extremities of the clypeus approximating the rectangular and grazing or nearly grazing the rim of the eye; the length of the clypeus about two-thirds its greatest width. The labrum very feebly bituberculate. The mandibles shaped somewhat like a thumb, their edentate apex narrower than their base but wider than in *pallida*, *chanchamayoensis*, and *amapana* and not so pointed as in those species. The malar space short but distinct on its outer half, but obsolete within, the inner angle of the base of

the mandible grazing the orbit of the eye. The distance between the lateral ocelli greater than that between each lateral ocellus and the nearest compound eye, the latter distance barely greater than the diameter of an ocellus. The carina behind the ocelli low and blunt. The appressed microscopic hairs on the clypeus, sides of face, front, vertex, and genal area (densely covering all but the lower extremity of this area) silvery gray. The erect hairs silvery gray to fulvous (fulvous, at least, on the vertex and sometimes even with black hairs intermixed with the fulvous in this area, exemplified by a specimen from Teffé). The erect hairs of the clypeus long and rather evenly distributed, notably longer than the inconspicuous hairs on the scape and rather longer, too, than the hairs on the front, but distinctly shorter than those of the vertex and shorter, too, than most of the erect hairs at the lower extremity of the genal area and an occasional longer hair fringing the mandibles below. The scape ferruginous with a sooty mark at the apex posteriorly; the flagellum dark above, usually a sharply contrasted ferruginous below.

THORAX: Ferruginous, the mesonotum usually a darker reddish than the sides or speckled with dark red or even largely or wholly blackish. Dense silvery gray appressed microscopic tomentum over all parts except the bare middle region of the propodeum. The erect hairs fulvous to here and there somewhat silvery gray but strongly fulvous (or even with intermixed blackish hair, a specimen from Teffé) on at least the scutellum. The hairs of the scutellum completely dwarf the hairs of the mesonotum and are longer, too, than those of the mesonotum and of the sides of the propodeum.

LEGS: Ferruginous to deeper red, with in one instance (a specimen from Teffé) the middle and hind metatarsi and the apical region of the hind tibiae even blackish. The hind tibiae (fig. 38E) moderately wide, almost straight along their anterior lateral contour, somewhat convex along their posterior lateral contour, the posterior part of the outer face somewhat flattened and towards the apex even somewhat concave; the contour of the apex of these tibiae irregularly rounded (more strongly rounded anteriorly than posteriorly, where they tend to be sub-

truncate); their greatest width (near the apex) nearly three-fourths that of the co-specific worker at the corresponding level. The hind metatarsi about four-fifths the width of the hind tibiae, the posterior apical extremity of these metatarsi subrectangular. The hairs of the legs prevailing fulvous to here and there brownish and sometimes even

hairs of the fringe about one-half as long as the hind tibiae are wide; the hairs fringing the hind metatarsi posteriorly distinctly long. The distribution of the simple fulvous hairs in general and their relative length approximate the specifications of the generalized description of the male of the subgenus *Trigona*.

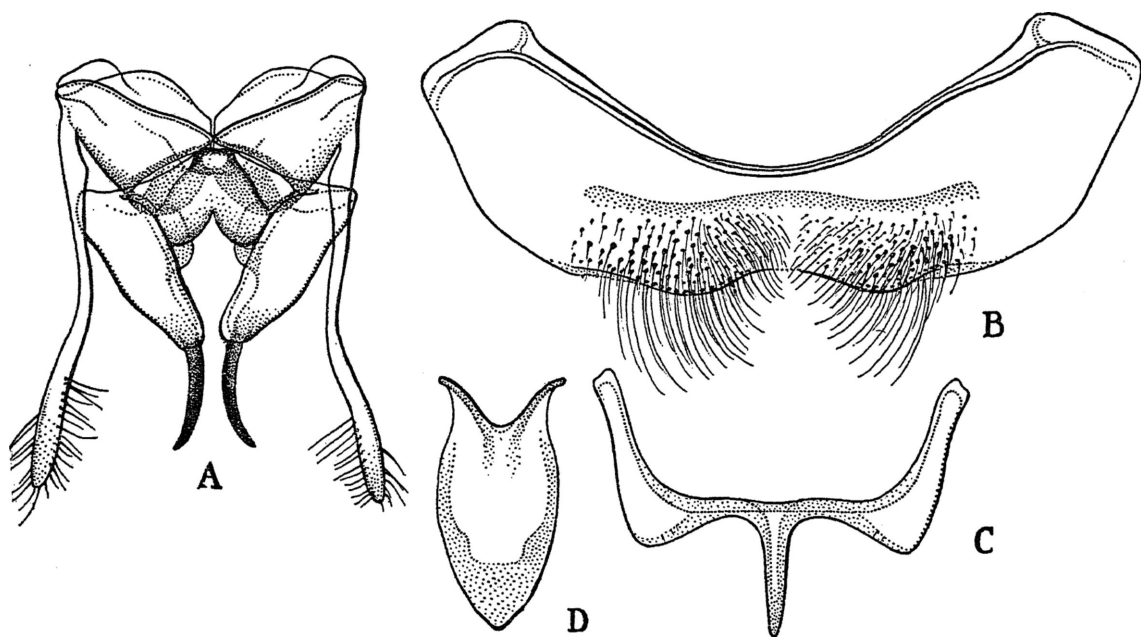


FIG. 44. Abdominal parts of male of *Trigona (Trigona) williana* Friese. A. Genitalia (chitinized parts only). B. Sternite 5. C. Sternite 6. D. Sternite 7. All based on a specimen from British Guiana. Drawings by Shirley H. Risser.

largely black (specimen from Teffé) but the following hairs whitish to silvery gray: the tomentum and other hairs on the under side of the trochanters, the dense fringe of very microscopic hairs on the under side of the femora, the microscopic but stubby hairs down the raised portion of the under side of the hind tibiae and the adjacent region at the apex of the under side of the hind femora, and the area of appressed sericeous hairs at the base of the under side of the hind metatarsi. The plumose hairs grayish, somewhat inconspicuous posteriorly on the outer face of the middle tibiae and usually rather dense and conspicuous over the outer face and along the posterior lateral contour of the hind tibiae, where they are far more abundant than the interspersed longer simple hairs; the simple

WINGS: With the coloration and venation described for the cospecific worker. Number of hamuli, in the eight wings available for examination, uniformly five.

ABDOMEN: Somewhat narrower than the thorax and, like that of the worker, sometimes ferruginous, in other cases more or less clouded, the darkened area sometimes confined or largely confined to the apical rim of the successive tergites but in other cases more pervasive. The hairs of the tergites fulvous. Tergite 1 devoid of hair; tergite 2 likewise with no or exceedingly few hairs and these apically; tergite 3 with a few short inconspicuous hairs along the apex and laterally; tergites 4 to 6 with longer, rather coarse erect hairs, particularly on tergites 5 and 6; tergite 7 fringed apically with some-

what incurved and moderately long hairs. The sericeous hairs of the sternites silvery white. For the structure of the tergites and genitalia, see figure 44.

MEASUREMENTS: Length about 8 mm.; width of thorax about 2.5 to 2.75 mm.; length of forewing, including tegula, 8.5 to 9 mm.

TYPE MATERIAL

Friese's type material embraced specimens from Surinam as well as Brazil. From the latter country the following localities were represented: Pará and Obidos in the State of Pará, Coary in the State of Amazonas, and State of Piahy. Type specimens were deposited in the Hungarian National Museum. Metatypes are in the possession of the American Museum of Natural History.

DISCUSSION

Trigona williana is readily separated from *dallatorreana* by its longer clypeus, its slightly bituberculate labrum (although not so pronounced as in *pallida*), by the contrast between its ferruginous clypeus and the usually darker sides of face, by its rather uniformly yellowish instead of hyaline to milky wings, by its ferruginous instead of usually blackened propodeum, as well as by other characters. To *pallida* it is structurally more closely related than to *dallatorreana*, but its much larger size makes confusion with *pallida* unlikely. In its facial markings *williana* particularly resembles *pallida* variety *ferricauda*, although this resemblance is probably not ascribable to mimicry as the two insects to only a slight extent encroach upon each other's domain, *ferricauda* having been reported up to the present only from Panama the Canal Zone, and Ecuador while *williana* is very possibly confined to South America.

Ducke (1916, p. 125; 1925, p. 413; 1945, p. 94) stated that at first glance *williana* reminds of *heideri* and other large species of Ducke's Group III. In spite of a superficial resemblance, however, *heideri* is structurally very different, lacking the smooth oval area at the base of the inner side of the hind metatarsi which characterizes both the worker and the male of *williana* and having an incompletely toothed mandible in contrast to the quinquedentate mandible of the worker of *williana*.

In describing the male of *williana*, Ducke (1916, p. 126; 1925, p. 414; 1945, p. 95) stated that "In some cases the entire head (including the antennae), the mesonotum, and a part of the pleura, black." This is a condition that is approximated in one of the males (from British Guiana, without more definite data) in the collections before me. Ducke's observation suggests that, as in *pallida* and *dallatorreana*, there may exist melanistic varieties of *williana*, although *williana* would seem on the whole to be much more stabilized in coloration.

The nest of *williana* is unknown.

Ducke (1902a, p. 420; 1902b, p. 304) collected *williana* on *Momordica charantia*.

A specimen of *williana* collected by M. A. Carriker at Río Mato, Caura District, Venezuela, bears a label with the following information: "Taken on trunk of a tree in forest on some gum, where there were many dead ones, covered with white mould" (cited by Cockerell, 1922, p. 8).

A field note by Lutz made in Kaieteur, British Guiana, and cited by Cockerell (1920c, p. 462) is to the effect that bees of this species "chew up human excrement and deftly pat it into balls on their hind legs." In Peru Weyrauch also observed *williana* visiting dung.

Specimens collected at Furo de Ressaco, on the Amazon, were obtained at night.

According to Le Cointe (1922, p. 383; 1945, p. 163), the honey of *williana* and of "some other related species, yellow and black, is sour, purgative, and of little use."

DISTRIBUTION

Friese (1900a, p. 388) included in the type region Surinam and localities in the Brazilian States of Amazonas, Pará, and Piahy. Ducke (1916, p. 126) expressed doubt as to the inclusion of the last-mentioned state but gave additional records for the States of Amazonas and Pará, and reported specimens also from Cuyabá in the State of Matto Grosso. Subsequently (1925, pp. 414-415) Ducke repeated these locality records but included Piahy without challenge. Ducke summarized the distribution as follows: "In the Hyläa present almost everywhere and in many localities even abundant; extends southward somewhat beyond the region men-

tioned." The range was extended when Cockerell reported *williana* from Abuna, Rio Madeira, in Acre Territorium, under the name *rhodoptera* (1912b, p. 49), from British Guiana (1920c, pp. 462-463; 1922, p. 8), and from Venezuela (1922, p. 8). The specimens in the collections before me indicate that the range of *williana* is even more extensive, for in addition to the countries mentioned the species is represented also in Ecuador, Bolivia, and Peru. The specimens here reported upon come from:

SURINAM: A type specimen of Friese.

BRITISH GUIANA: Bartica, May 17, 1901, Aug. (Pomerat); Rockstone, Essequibo River, March 23, 1913 (G. E. Bodkin); Aracara Cataract to Popikai Falls, Mazaruni River, Aug. 15, 1920 (R. E. Wheeler); Mary's Falls to Kaburi Rock, Mazaruni River, Aug. 17, 1920 (R. E. Wheeler); Kartabo, Aug. 5, 1920, and Aug. 9, 1920, male (W. M. Wheeler), Oct. 16, 1920, and Oct. 22, 1920 (W. Beebe); Mt. Everard, Nov. 15, 1922; Arakaka, Dec. 21, 1922; Kamakusa, Jan., 1923 (H. Lang); Matope, July 23, 1924 (J. F. W. Pearson); Camaria, July 31, 1924 (Pearson); Kangaruma, May 23, 1929 (J. Ogilvie); Tumatumari, May 23, 1929 (A. Mackie); Essequibo River, Moraballi Creek, Sept. 22, 1929, and Oct. 3, 1929 (Oxford Univ. Exped.); Mabaruma, Northwest District, Feb., 1931 (J. G. Myers); Yarikita, Northwest District, Feb., 1931 (J. G. Myers); Forest Settlement, Mazaruni River, Aug.-Sept., 1935 (N. A. Weber); Waranama, Nov. 16, 1936, and Nov. 19, 1936 (J. Ogilvie); Kuyuwini River, Nov. 22, 1937 (W. G. Hassler); upper Essequibo River, Dec. 23, 1937 (W. G. Hassler).

VENEZUELA: Río Mato, Caura District, Oct., 1909 (M. A. Carriker); Río Amacuro, Feb., 1931 (J. G. Myers).

BRAZIL: State of Amazonas: Faro, 1890 (Schulze), and Dec., 1905; Teffé, male, Sept., 1904 (Ducke), and Dec. 7, 1919, and Jan. 28, 1920 (H. Parish); Flores, Manáos, Aug. 4, 1924 (J. Bequaert); S. Alberto, Rio Branco, Aug. 15-25, 1924 (J. Bequaert); Carmo, Rio Branco, Aug. 21, 1924 (J. Bequaert); Manáos, March, 1945 (W. Praetorius); Furo de Ressaco, Rio Amazon, Sept. 10, 1920, at night (Cornell Univ. Exped.). State of Pará: Santarem (H. H. Smith). State of Matto Grosso: Chapada (presumably Sant' Anna do Chapada, near Cuyabá); Corumbá.

BOLIVIA: Ivon, Río Beni, Feb. (W. M. Mann).

PERU: Iquitos, May 8, 1920 (H. Parish), and Aug. 7, 1920 (Cornell Univ. Exped.); Río Putumayo, Aug. 14, 1920 (Cornell Univ. Exped.); La Sombra, Aug. 22, 1920 (Cornell Univ. Exped.);

Río Tapiche, Dec. 14, 1923 (H. Bassler); Valle de Chanchamayo, 800 meters, 1939, No. 145 (W. Weyrauch); Satipo, 600 meters, Aug. 10, 1940 (W. Weyrauch).

ECUADOR: Tena, Feb. 23, 1923, and March 27, 1923 (F. X. Williams).

Trigona (Trigona) dallatorreana Friese

Trigona dallatorreana FRIESE, 1900a, pp. 387-388.

Melipona dallatorreana, DUCKE, 1902a, p. 420.

Melipona (Trigona) dallatorreana, DUCKE, 1902b, pp. 290, 301-302.

Trigona Dallatorreana, DUCKE, 1907, p. 89.

Trigona dallatorreana, MARIANNO, 1911, pp. 90-91.

Melipona dallatorreana, DUCKE, 1916, p. 13, opposite p. 28, pp. 31, 72-74, 75, pl. 5, fig. 15.

Trigona dallatorreana, COCKERELL, 1920c, p. 463.

Trigona dallatorreana, LUTZ, 1924a, pp. 205, 207, 210, 216.

Melipona dallatorreana, DUCKE, 1925, pp. 343, 351, 384-385, 386, text fig. P, pl. 4, fig. 12.

Trigona dallatorreana, SCHWARZ, 1932a, pp. 253, 256.

Trigona (Trigona) dallatorreana, SCHWARZ, 1938, pp. 438, 443, 459-460, pl. 52, figs. E, E1, pl. 53, figs. G, H.

Melipona dallatorreana, DUCKE, 1945, p. 13, opposite p. 24, pp. 56, 58, 59, pl. 5, fig. 15.

WORKER

DIAGNOSTIC CHARACTERS: Mainly fulvous but variably invaded with black. Mandible five toothed. Length of malar space about equal to width of flagellum. Clypeus rather flat, without median channeling, and barely or not at all foveate apically, notably short compared to its width, which is fully three times as great as the length. Bristles fulvous on clypeus, supraclypeus, and scape. Labrum simple. Facial quadrangle distinctly wide, wider than long. Hind tibiae notably wide, with an inwardly placed angle posteriorly at the apex. Wings rather uniformly milky, without a trace of a dark or a yellowish tinge.

HEAD (FIG. 37E): Sometimes wholly or almost wholly fulvous as are the other parts of the body, but frequently more or less invaded by black or brown (details of variability follow below). The facial quadrangle very notably wide, the distance between the compound eyes at a level just below the middle ocellus a little greater than the distance from the middle ocellus to the apex or

the clypeus, about in the proportion of 10 to 9. The eyes distinctly convergent below, the distance that separates them at their level of greatest approximation (below) being about as 8.25 is to 10 compared with the distance between them at a level just below the middle ocellus. The length of the eye about equal to the shortest distance between the eyes. The clypeus raised only a little above the level of the sides of the face and rather flat, without median channeling and barely or not at all foveate apically; the clypeus notably short compared to its width (measured from one apico-lateral extremity to the other), which is fully three times as great as the length. Each anterolateral extremity of the clypeus separated from the nearest compound eye by very nearly the width of the flagellum. The labrum simple (not bituberculate), of rounded contour to obtusely triangular. The mandibles armed with five teeth, the two innermost small. The malar space, measured from the lower extremity of the eye to the middle of the base of the mandible, about as long as the flagellum is wide. The distance between the lateral ocelli distinctly less than that separating each lateral ocellus from the nearest compound eye. The carina behind the ocelli blunt but moderately distinct. The silvery gray appressed hairs almost as dense on the clypeus as they are on the sides of face, front, and vertex; the genal area silvery gray pruinose (more whitish viewed from some angles, more yellowish viewed from others). The longer hairs mostly rather coarse and fulvous; those on the clypeus strongly down-slanting, inconspicuous, more numerous on the lower half of the clypeus than on the upper half; those on the supraclypeus rather more erect; those on the inner face of the scape approximating in length the width of the scape and rather longer than those on the lower half of the clypeus; those on the front distinctly longer than those of the clypeus but distinctly shorter than those of the vertex and mandibles below; some short hairs usually emerging among the silvery gray appressed hairs on the sides of face and upper two-thirds of genal area; the labrum with a few rather long hairs that more or less approach in length those on lower one-third of genal area. Sometimes the front wholly fulvous but

in other cases there is a black (or brown) more or less shield-shaped maculation coextensive in width with the ocelli, to which it is contiguous; this maculation usually makes contact (below) with the upthrust fulvous summit of the supraclypeus, and there either terminates or forks, extending a branch along each of the sides of the supraclypeus towards the antennal sockets. Specimens thus maculated almost invariably have, in addition, a narrow, medianly interrupted crescent of black posterior to the ocelli; each horn of the crescent points to the summit of the eye nearest to it; posterior to the crescent, there is almost always on the occiput of such specimens a second dark streak, the ends of which are only slightly divergent from the horns of the crescent. (Specimens with this type of maculation, fig. 37E1, are present from Kartabo, British Guiana, from Pará, Brazil, from Tarata and Osunto in Bolivia, and from El Campamento and Dos de Mayo to El Porvenir in Peru). The clypeus is not infrequently rimmed more or less with black, and sometimes this rimming penetrates so deeply that virtually the entire clypeus is black except for two subparallel longitudinal fulvous stripes (some of the specimens from El Campamento, Peru). The malar space and the lower extremity of the genal area are apt to be cloudy to blackish, particularly in the case of specimens having the other black markings mentioned. The mandibles are fulvous, but are suffused with red towards the apex and have the teeth and the basal prominences black.

THORAX: Predominantly fulvous but, like the head, invaded by black to a variable extent. Almost always (Frieese uses the term "often") at least the bare shiny middle area of the propodeum is black or strongly cloudy (specimens from Ivon, Río Beni, Bolivia, are an exception, but these specimens show also a bleached appearance of the stigma and are in all probability callows). In not a few cases there is on the lower posterior half of the mesopleura a large black spot and the area below the hind wings is similarly black (specimens from Porto América on the Río Putumayo, Faro in the State of Amazonas, Pará in the State of Pará, some specimens from Chapada in the State of Matto Grosso, Osunto and Tarata in Bolivia, El Campa-

mento and Dos de Mayo to El Porvenir in Peru, Kartabo and Bartica in British Guiana, and Mt. Duida in Venezuela). More rarely, the mesonotum has two broad dark stripes, posteriorly diverging, that traverse it and divide it into three subequal areas, the middle area red, the lateral areas somewhat clouded (some specimens but not all from El Campamento, Peru, and specimens from Kartabo and Bartica, British Guiana). Such specimens

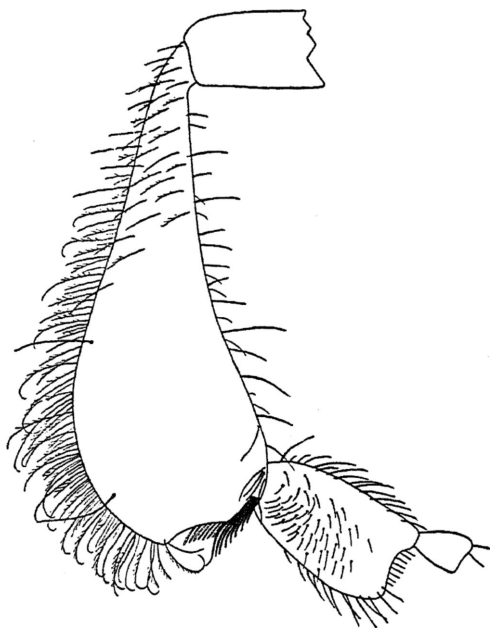


FIG. 45. Hind tibia and metatarsus of worker of *Trigona* (*Trigona*) *dallatorreana* Friese. Drawing by Elena Feld.

are apt to have the scutellum black, but a black scutellum as well as black axillae is associated sometimes with specimens that have a purely fulvous mesonotum (specimens from Pará and several of those from Osunto, Bolivia). The mesonotum, scutellum, mesopleura, and sides of propodeum covered with a very dense gray to whitish tomentum that dulls their shininess, and in addition there are abundant silvery to fulvous hairs in these areas. The hairs of the mesonotum a little shorter than those of the scutellum, but those anteriorly on the mesonotum not notably different in length from those more medianly placed. The scutellum very broadly rounded posteriorly.

LEGS: Fulvous but not infrequently with variable amounts of black. In extreme cases (specimens from El Campamento, one specimen from Pará, and some of the British Guiana specimens) the following parts are black: the under side of all the femora and a streak along the upper side of the middle and hind pair; the apex of both the outer and inner sides of the front and middle tibiae, supplemented by a streak running lengthwise on the outer side of the middle tibiae; the hind tibiae on both the inner and outer faces except for a fulvous area anteriorly about the middle of the joint (fig. 38H); and all of the metatarsi. (Specimens with dark markings on the head are apt to have dark markings on the legs, but in varying degree sometimes even within the same locality.) The hind tibiae clavate (fig. 45) in outline, considerably wider at the apex than at the base, their anterior lateral contour moderately concave, their posterior lateral contour strongly convex; their apex with an angle anteriorly that bears the tibial comb; beyond this angle there is a slight bulge in the apical contour followed by an emargination that culminates in a somewhat inwardly placed angle where this emargination encounters the posterior contour of the joint. The outer face of the hind tibiae very gently arched over the basal two-thirds, especially anteriorly, and flattened to moderately depressed over the apical one-third, especially posteriorly. The flattened area that constitutes the posterior part of the inner face of the hind tibiae fully two-fifths as wide towards the apex as the joint is wide. The hind metatarsi about three-fifths as wide as the hind tibiae at their widest, their apex posteriorly approximating the rectangular. The hairs of the legs fulvous except for the dense fringe of very microscopic whitish hairs usually traceable on the under side of the femora, the pale plumose hairs on the outer face of the middle tibiae and adjacent area at the base of the middle metatarsi, the microscopic but stubby silvery gray hairs on the raised portion of the under side of the hind tibiae and over the adjacent part of the apex of the hind femora beneath. The suboval bristleless patch at the base of the under side of the hind metatarsi silvery gray to whitish sericeous when not concolorous with the fulvous chitin due to its being

glazed over with sticky matter. The relative length of the hairs and their distribution as noted in the description of the worker of the subgenus *Trigona*.

WINGS: Rather uniformly milky, without a trace of a dark or a yellowish tinge. The venation, stigma, and tegulae pale ferruginous, the stigma sometimes even whitish. Venation in lower and apical part of forewing and over much of hind wing rather unusually feeble. Marginal vein with a tendency to fade out towards its apex. Transverse cubital veins barely or not at all traceable. The first discoidal cell about seven-tenths as long as the marginal cell. Number of hamuli on hind wing usually five, sometimes six or four. Of 76 wings examined, 66 had five hamuli, five had four hamuli, and five had six hamuli, an average of 5.

ABDOMEN: Considerably narrower than the thorax, usually rather elongated, with the segments rather fully exposed instead of telescoped, and tergites 5 and 6 tending to be vertical in position. The color of the abdomen highly variable, with many transitions: sometimes entirely or almost entirely black except for the basal segment and the apical segment (specimens from Mt. Duida in Venezuela and from Porto América on the Rio Putumayo), sometimes blackish to reddish with stramineous apical bands (specimens from Pará and Faro, Brazil, from Ivon, Río Beni, Tarata, and Osunto, Bolivia); sometimes reddish streaked with black (specimens from Chapada, Brazil, and from El Campamento and Dos de Mayo to El Porvenir in Peru). The hairs fulvous: a few microscopic appressed hairs on the apex of tergite 2; the hairs along the apex of tergite 3 for the most part similarly appressed but with a few semi-erect hairs usually in the middle region; tergites 4 to 6 with much longer and coarser hairs, those on tergite 4 confined largely to the middle region of the apex, those on tergite 5 numerous on the sides as well as especially on the middle region of the apex, those on tergite 6 (the longest of all) over all of the exposed part of the tergite. The abdomen smooth and shiny, but very faint traces of tessellation on the apex of tergites 2 and 3, and the hairy areas of the subsequent tergites granular where the hairs emerge. The hairs of the under side of the abdomen not nearly so

coarse as those of the dorsal side and on the whole a little paler; the longer hairs occur at the middle of the apex of each of the successive sternites and are flanked on sternites 3 to 5 by glistening dense sericeous patches that are silvery gray seen from certain angles and yellowish when viewed from others.

MEASUREMENTS: Length 7 to 9 mm.; width of thorax 2.25 to 2.5 mm. (Friese gives 2.25 mm. as the width); length of forewing, including tegula, 7.25 to 8 mm.

QUEEN

Unknown.

MALE¹

HEAD: Fulvous and wide; its length about five-sevenths that of its width. The facial quadrangle relatively wide. The distance from one eye to the other at their level of closest approximation is about two-thirds of the length of the eye. The eyes relatively narrow for a male *Trigona*, not so wide as the genal area, and strongly convergent below, the distance between the eyes at the level just below the middle ocellus being about equal to the distance from the middle ocellus to the apex of the clypeus, but at their level of closest approximation (below) the distance separating the eyes is only about two-thirds that of their divergence at the level just below the middle ocellus. The clypeus, at least, barely raised above the level of the sides of the face, the supraclypeus a trifle more prominent; the apico-lateral extremities of the clypeus rectangular and separated from the rim of the eye by less than the width of the tapering flagellum towards the apex; the length of the clypeus only about one-half its width. The labrum simple. The otherwise fulvous mandible with a darkened inwardly receding apex that is almost as wide as the base of the mandible; this apical edge with a notch at the middle and with a small denticle at its inner extremity, otherwise virtually without evidence of teeth. The malar space distinct, although its length at the middle is rather less than the width of the slightly tapering flagellum towards its apex. The middle ocellus separated from each of the

¹ This description is based on a single specimen from Río Marañón, Peru.

lateral ocelli by about the diameter of an ocellus; the lateral ocelli more widely separated from each other than either is separated from the compound eye, the distance intervening between a lateral ocellus and the nearest compound eye being, however, relatively great, fully twice the diameter of an ocellus. A blunt carina behind the ocelli. The hair dense, abundant, and rather coarse, tending partly to conceal the shiny integument, even the tomentose hairs (except those of the genal area, which are silvery gray pruinose) only feebly silvery gray in some lights, in others more fulvous, and the longer hairs distinctly fulvous. The down-sloping fulvous hairs on the clypeus are long, emphatically longer than the hairs of the scape, which themselves approximate the width of the scape. The hairs towards the top of the front also distinctly long, although the hairs of maximum length occur on the vertex and towards the base of the under side of the mandibles. The hairs likewise long on the labrum and on the lower extremity of the genal area. The scape and the flagellum below fulvous, the flagellum above very slightly darkened.

THORAX: Predominantly fulvous but with a black spot posteriorly on the lower half of the mesopleura and the propodeum (particularly the bare middle area) blackened. The mesonotum a little wider at the base than it is long, about in the proportion of 9 to 7, but the combined length of mesonotum and scutellum somewhat greater than the maximum width of the mesonotum. The hairs fulvous and coarser and longer than is the case in the conspecific worker, the hairs of the mesonotum in particular being relatively long for that area and little differentiated in length from the hairs of the scutellum. Fulvous to silvery gray tomentum present in addition to the longer simple hairs, densely so on the mesonotum, on the mesopleura, and at each side of the bare middle area of the propodeum.

LEGS: Fulvous, with slight cloudiness on the outer face of the middle metatarsi, apex of hind femora, external face of the hind tibiae with the exception of a fulvous area anteriorly about the middle of the joint, and the external face of the hind metatarsi. The hind tibiae wide, their anterior lateral con-

tour slightly concave, their posterior lateral contour strongly convex (particularly on the apical one-half); accordingly the joint is much wider at the apex than at the base. The anterior part of the outer face of the hind tibiae rather strongly arched, the posterior part of the outer face gradually flattened towards the apex. The apical margin of these tibiae gently rounded on their anterior half, subtruncate to barely emarginate on their posterior half, forming a feeble angle where this apical contour joins the apex of the posterior lateral contour. The greatest width of these tibiae (near the apex) fully four-fifths as wide as the corresponding joint of the worker at the same level. The hind metatarsi somewhat under two-thirds the width of the associated tibiae, the posterior apical extremity of these metatarsi barely acute. The hairs for the most part more or less concolorous with the chitin, tending to be yellowish in the fulvous areas and somewhat more brownish in the slightly darker areas. The hairs on the under side of the middle trochanters denser and of a more fulvous tinge than the rather pale hairs on the under side of the fore and hind trochanters. A dense fringe of very microscopic whitish hairs on the under side of the femora with some slightly longer hairs as well. The inner face of the hind femora (particularly towards the apex) with a longitudinal stripe of dense silvery gray microscopic hairs that is virtually continuous with a similar hirsute stripe down the sharp elevation on the under side of the hind tibiae. Plumose hairs absent or virtually absent from the outer face of the middle and of the hind tibiae (where for the most part only erect simple hairs occur), but a dense, rather pale fringe of plumose hairs, intermixed with sparser but longer fulvous to darker simple hairs, occurs along the posterior lateral margin of the hind tibiae. The hairs on the outer face of the middle tibiae and fringing these tibiae posteriorly erect and rather exceptionally long compared with the hairs on the outer face of the fore tibiae. The fringe of the posterior lateral contour of the hind tibiae well developed, the length of the simple hairs of this fringe fully one-half the width of the joint. The suboval, bristleless area at the base of the under side of the hind metatarsi silvery gray to whitish seri-

ceous. The distribution of the simple hairs in general and their relative length approximately as indicated in the generalized description of the male of the subgenus *Trigona*.

WINGS: Hyaline, rather uniformly milky, with yellowish to orange venation, stigma, and tegulae. Number of hamuli per hind wing, in the only specimen before me, five.

ABDOMEN: Narrower than the thorax, subcylindrical, predominantly fulvous. Tergites

as well as from Pará, Brazil. From the last-mentioned locality there are in the American Museum of Natural History four workers, all bearing date September, 1900 (Ducke), and identified by Friese as *dallatorreana*. Although collected in the same year that Friese's paper was published, these four specimens are to be regarded as metatypes rather than as paratypes, for they post-date the appearance of Friese's article by a month.

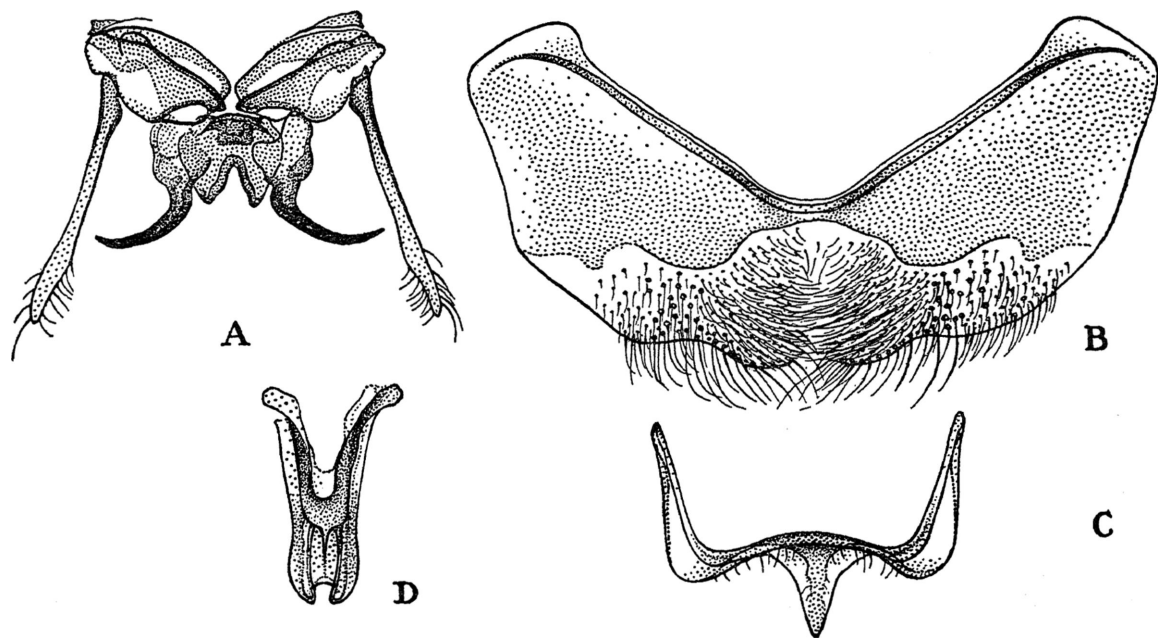


FIG. 46. Abdominal parts of male of *Trigona (Trigona) dallatorreana* Friese. A. Genitalia (chitinized parts only). B. Sternite 5. C. Sternite 6. D. Sternite 7. All based on a specimen from Río Marañón, Peru. Drawings by Shirley H. Risser.

1 and 2 virtually hairless; tergite 3 with appressed fulvous hairs along its apex; the subsequent tergites with more erect and longer fulvous hairs over their exposed apical half. The sternites silvery gray sericeous. For the structure of the sternites and genitalia, see figure 46.

MEASUREMENTS: Length about 7 mm.; width of thorax about 2.5 mm.; length of forewing, including tegula, about 7 mm.

TYPE MATERIAL

The type material of *dallatorreana* was of widely scattered origin. There were specimens from Surinam, from Peru (Pebas),

There is also a metatype from Tarata, Bolivia, in the American Museum. The Hungarian National Museum is the depository of the original type material.

DISCUSSION

As the description of the worker indicates, the coloration of this species is very variable. Even in Friese's original description some variability is noted, and Ducke and Marianno in their more detailed descriptions gave additional instances of variability. Ducke (1902b, p. 301) stated that in specimens from Peru he did not note the dark maculation below the ocelli and the black lines on the

top of the head which he found characteristic of all specimens from Pará, but according to my own observations these dark maculations are present also in specimens from some localities not only in Peru but also in Bolivia. Ducke likewise referred (1902b, p. 302) to the dark maculations on the legs of specimens from Pará, but, as is indicated in the present description, this distinction is shared by specimens from other localities. The variability in *dallatorreana* is indeed particularly elusive. Specimens illustrating in varying degree one extreme or another have a very spotty geographical distribution and are without fixity even within a single locality (for example, specimens with dark maculations on the mesonotum as well as specimens without such maculations were obtained at El Campamento, Peru). In general, specimens that have black maculations on the head are apt to have black maculations also on the legs, but the specimens before me that have the greatest prevalence of black on the abdomen (those from Pôrto América on the Rio Putumayo) have, curiously enough, unsoiled head, legs, and mesonotum. Where there are so much instability and a geographic distribution so haphazard, it seems perhaps preferable to depart from the principle observed in general in this paper of establishing named varieties of a species and merely to call attention, as was done in the description, to the different manifestations.

For the differences between *dallatorreana* and *williana* the reader is referred to the latter species (p. 319).

Ducke (1902a, p. 420; 1902b, p. 302) encountered *dallatorreana* in numbers on *Amaranthus spinosus*. On another occasion he found part of a nest that had been established in an arboreal termite structure. In referring to this nest later Ducke (1916, pp. 73-74; 1925, p. 385; 1945, p. 58) indicated that the nest was in fragments because of its having fallen with the branch to which the termite structure was attached. Ducke added: "I do not recall that the interior architecture was different from the usual type (involucrum and combs present)."

Like *williana* the present species was collected by night at Furo de Ressaco, on the Amazon River.

DISTRIBUTION

Friese (1900a, p. 388) based his description of *dallatorreana* on specimens from Brazil, Dutch Guiana, and Peru. Cockerell (1920c, p. 463) added Bolivia to the known range. Ducke (1925, p. 385) stated that the species extends through "the entire Hyläa region but is probably everywhere rather rare." He listed localities in Surinam, in the Brazilian States of Pará, Amazonas, and northern Matto Grosso, and in eastern Peru.

In the collections before me the following localities are represented:

BRITISH GUIANA: Kartabo, July 27, 1920, and Aug. 18, 1920 (W. M. Wheeler), July 11, 1922, and July 23, 1926 (W. Beebe); Bartica, April 26 (W. Beebe); Essequibo River, at source (J. Ogilvie).

VENEZUELA: Mt. Duida, Nov. 4, 1928 (G. H. H. Tate).

BOLIVIA: Tarata, 1900; Ivon, Río Beni, Feb. (W. M. Mann); Tumupasa, Dec. (W. M. Mann); Osunto, July (G. Macreagh).

PERU: El Campamento, Colony of the Perené, June 21, 1920 (Cornell Univ. Exped.); Dos de Mayo to El Porvenir, Cam. del Pichis, July 6, 1920 (Cornell Univ. Exped.); Iquitos (H. Bassler); middle Río Ucayali, Aug. 31, 1923, Nov. 19, 1923 (H. Bassler); Río Tapiche, Dec. 14, 1923 (H. Bassler); Río Marañon, Sept. 25, 1924, male (H. Bassler).

BRAZIL: State of Amazonas: Faro, Dec., 1905; Pôrto América, Rio Putumayo, Aug. 30-Sept. 12, 1920 (Cornell Univ. Exped.); Furo de Ressaco, Rio Amazon, night, Sept. 10, 1920 (Cornell Univ. Exped.). State of Pará: Pará, Sept., 1900 (Ducke). State of Matto Grosso: Chapada (probably Sant' Anna do Chapada, which is near Cuyabá).

Trigona (Trigona) braueri Friese

Trigona braueri FRIESE, 1900a, p. 387.

Melipona braueri, DUCKE, 1916, pp. 123-125.

Melipona braueri, DUCKE, 1925, p. 413.

Melipona braueri, DUCKE, 1945, pp. 93-94.

WORKER

"Worker.—Related to the well known *M. williana*, but much smaller (of middle stature, with short abdomen) and with a moderate emargination along the posterior contour of the hind tibiae. Body without sculpturing, fairly shiny, pale rust yellow; vertex and dorsal aspect of thorax somewhat darker and without much gloss; sides of face along the

orbits brownish and dull; head and thorax in large part with white tomentum; vertex, dorsum of thorax, and apex of abdomen with fairly well developed erect brownish gray hairs. Head only a little wider than the thorax but genal area fairly wide; malar space rather strongly developed; mandible four-toothed. Scutellum with a plain rim, little salient; the middle area of the propodeum bare and shiny. Abdomen strongly shiny, in its basal part almost bare. Hind tibiae moderately widened, rounded at the end, excavated on their outer face over about one-third of the apex, posterior contour convex but with a distinct emargination before the middle, of moderate length but with very dense yellowish gray hair, anterior contour concave; hind metatarsi scarcely narrowed at the base. Wings long, yellowish hyaline with pale yellowish venation. Body length 5-6 mm., thorax width 2 mm." (Ducke, 1925, p. 413).

QUEEN

Unknown.

MALE

Lumped by Friese with the worker in his brief description (1900a, p. 387), but the structural characters which Friese gives are those of the worker.

TYPE MATERIAL

Friese (1900a, p. 387) based his description on six workers and four males from Santa Leopoldina in the State of Espirito Santo, Brazil. He added that in the Vienna Museum are numerous specimens also from the Brazilian State of Bahia.

DISCUSSION

The above description is a translation of the redescription in German offered in 1925 (p. 413) by Ducke, which itself is in turn a translation, with slight transposition of some of the phrases, of the description in Portuguese written by Ducke in 1916 (pp. 123-124). Friese's original description (1900a, p. 387) is briefer. The description of Friese as well as the redescriptions of Ducke specifies the number of teeth on the mandible as four, which, if correct, suggests affiliation of

braueri with such bees as *fulviventris* Guérin and *compressa* Latreille. On the other hand, Ducke, at least, refers to *williana* as four toothed (1916, p. 125; 1925, p. 414; 1945, p. 95), whereas *williana* has, in fact, five teeth. As Ducke thinks *braueri* is close to *williana*, it is possible that an error has been made also in the count of the teeth of *braueri*.

It would seem that *braueri*, of which I have no specimens, is an outpost species that, while sharing the completely toothed mandible characteristic of members of the subgenus *Trigona*, nevertheless has certain resemblances, too, to those representatives of the subgenus *Tetragona* that have the apical half of the hind tibiae somewhat abruptly expanded. In Ducke's key (1925, p. 354) *braueri* is separated from other bees assignable to the subgenus *Trigona* by the character of its hind tibiae, described as "convex, but with their posterior rim gently emarginate before the middle," and it is this character which is again later (1925, p. 413) alluded to by Ducke as distinguishing *braueri* from its near relatives and inclining it towards certain members of Ducke's Group III, a rather miscellaneous group in which, however, subgenus *Tetragona* is more or less predominant.

The nest of *braueri* is unknown.

DISTRIBUTION

Ducke (1916, p. 124; 1925, p. 413; 1945, p. 94) lists the Brazilian States of Bahia and Espirito Santo, without expanding the range reported by Friese (1900a, p. 387).

Trigona (Trigona) fulviventris variety *fulviventris* Guérin

Trigona fulviventris GUÉRIN, "1829-1844," p. 464.

Trigona fulviventris, GOUDOT, 1846, p. 713.

Trigona laboriosa F. SMITH, 1862, p. 42.

Trigona fulviventris, GIRARD, 1879, p. 724.

Trigona fulviventris, GRONEN, 1881b, p. 332.

Trigona fulviventris, GRONEN, 1881c, p. 111.

Melipona fulviventris, DALLA TORRE, 1896, p. 579.

Melipona fulviventris, DUCKE, 1901, pp. 26, 31, 32, 51, 64.

Melipona fulviventris, DUCKE, 1902a, pp. 323, 325, 419, 420.

Melipona (Trigona) fulviventris, DUCKE, 1902b, pp. 312-313, pl. 11, fig. 6.

Trigona fulviventr, GRÜNBERG, 1904, pp. 9, 15, 17.

Trigona fulviventr, SCHULZ, 1904b, p. 826.

Trigona fulviventr, DUCKE, 1906b, pp. 52, 53.

Trigona fulviventr, DUCKE, 1907, p. 89.

Melipona fulviventr, RUDOW, 1907, p. 30.

Trigona fulviventr, DUCKE, 1908b, p. 80.

Trigona fulviventr, COCKERELL, 1910c, p. 366.

Trigona fulviventr, MARIANNO, 1911, pp. 8, 24, 31, 35, 40, 47, 49, 53, 97-98, 127, pl. 4.

Trigona fulviventr, COCKERELL, 1912b, p. 61.

Trigona fulviventr, COCKERELL, 1912c, p. 314.

Trigona fulviventr, COCKERELL, 1913a, p. 10.

Trigona fulviventr, WHEELER, 1913, p. 4 (identified by T. D. A. Cockerell).

Melipona fulviventr, RUDOW, 1914, p. 241, fig. 10.

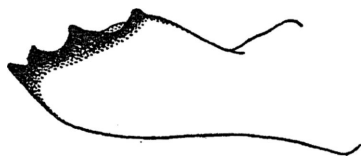


FIG. 47. Mandible of worker of *Trigona* (*Trigona*) *fulviventr* variety *fulviventr* Guérin. Drawing by Alice Gray.

Melipona argentata aberration *fulviventr*, DUCKE, 1916, pp. 128-129.

Trigona fulviventr, FRIESE, 1917, pp. 289, 299.

Trigona fulviventr, COCKERELL, 1920c, p. 461.

Trigona fulviventr, LUTZ AND COCKERELL, 1920, p. 498.

Trigona fulviventr, WHEELER, 1923, p. 122.

Trigona fulviventr, LUTZ, 1924a, pp. 205, 207, 209, 216.

"A red-bellied *Trigona*," LUTZ, 1924b, pp. 495, 508.

Melipona argentata aberration *fulviventr*, DUCKE, 1925, pp. 416-417.

Trigona fulviventr, BOUVIER, 1926, p. 39.

Trigona fulviventr, L. E. CHEESMAN, 1929, p. 150.

Melipona fulviventr, GUENTHER, 1931, p. 376.

Trigona fulviventr, BEQUAERT, 1932, p. 17.

Melipona argentata aberration *fulviventr*, ALFKEN, 1932b, p. 306.

Trigona fulviventr, SCHWARZ, 1932a, pp. 253, 256.

Trigona fulviventr, RAU, 1933, pp. 16, 27, 38 (identified by Grace Sandhouse and by H. F. Schwarz).

Trigona fulviventr, SCHWARZ, 1934, pp. 3, 12-13.

Trigona fulviventr, MAIDL, 1934, p. 167.

Melipona pulviventr (*sic*), R. VON IHERING, 1940, p. 297.

Trigona (*Trigona*) *fulviventr*, VON HAGEN, 1943, p. 44.

Melipona argentata aberration *fulviventr*, DUCKE, 1945, pp. 97-98.

Trigona fulviventr, MICHENER, 1946, pp. 180, 181, 185, 189-190 (identified by H. F. Schwarz).

WORKER

DIAGNOSTIC CHARACTERS: Black with a fulvous to reddish abdomen. Mandible four toothed, for the most part reddish. Length of malar space nearly equal to width of flagellum. Clypeus smooth and even, without a fossa bisecting it and not apically foveate, its length somewhat less than half its greatest width. Erect black hairs on clypeus, supraclypeus, and scape, those on scape short. Labrum with two fairly distinct prominences. Hind tibiae with an inwardly placed angle posteriorly at the apex; the outer face of these tibiae rather strongly depressed over the apical two-fifths. Wings subtransparent, with a much diluted yellow stain that is of uniform tinge throughout.

HEAD: Black or mainly black. The facial quadrangle moderately wide, the distance between the compound eyes at a level just below the anterior ocellus being somewhat less (in the proportion of about 7.5 to 9) than the distance from the anterior ocellus to the apex of the clypeus. The compound eyes somewhat convergent below, the distance that separates them at their level of greatest approximation (below) being about as 6.75 is to 7.5 when compared with their divergence near the summit. The clypeus raised a little above the level of the sides of the face, but smooth and even, devoid of median channeling and not foveate apically; its width, measured from one apico-lateral extremity to the other, a little more than twice its length; each anterolateral extremity of the clypeus separated from the nearest compound eye by about one-half the width of the scape. The supraclypeus no more prominent than the clypeus. The labrum with two more or less distinct tubercles. The mandibles (fig. 47) armed with *four* teeth (not five as in most of the species of the subgenus *Trigona*), the fourth and innermost being rather widely separated from the preceding three and less developed, often subtooth-like. The malar space, measured from the lower

extremity of the eye to the middle of the base of the mandible, nearly as long as the flagellum is wide. The distance between the lateral ocelli somewhat less than that which separates each lateral ocellus from the nearest compound eye. The carina behind the ocelli moderately developed. Fine, appressed, silvery gray microscopic hairs of considerable density on the sides of the face, of moderate density on the clypeus, front, and vertex, and of concealing density on the upper two-thirds of the genal area, where the tinge is sometimes slightly olivaceous, depending on the angle at which the insect is held. All the erect hairs of the head black except for those fringing the lower edge of the mandibles, which are apt to be copper colored. The black hairs over the clypeus and supraclypeus relatively long, almost as long as those on the front; the scape has hairs that are shorter than the scape is wide. The hairs on the vertex, mandibles below, and lower one-third of genal area longer than the other hairs of the head and a few long hairs also on the labrum. Sparse microscopic erect black hairs usually scattered among the silvery gray appressed hairs in the region adjoining the inner and outer orbits of the eyes. The clypeus and supraclypeus somewhat variable in coloration, sometimes black like the rest of the head, in other cases more or less invaded by reddish brown or entirely of that color, approximating in such cases the color of the reddish labrum and of the mandibles, which, except for their usually black teeth and black basal prominences, likewise tend to be reddish. The scape and flagellum dark above, brownish below.

THORAX: Black or blackish, its sides sometimes more or less suffused with reddish. The mesonotum, scutellum, pleura, and sides of propodeum with their sheen subdued owing to the presence over these areas of rather dense dull gray to rather lusterless silvery grayish tomentum. The erect hairs in these areas black, their relative length as indicated in the description of the subgenus *Trigona*.

LEGS: Usually black, frequently with more or less reddish brown suffusion and at least the apical tarsal joint usually rather bright ferruginous. The hind tibiae clavate in outline, considerably wider at the apex than at the base; their anterior lateral contour gently

emarginate; their posterior lateral contour strongly convex; their apex with an inconspicuous angle anteriorly that bears the tibial comb; beyond this angle there is a slight bulge in the apical contour followed by an emargination that results in a somewhat inwardly placed angle where this emargination encounters the posterior lateral contour of the joint. The outer face of the hind tibiae (fig. 48) very gently arched to almost flat-

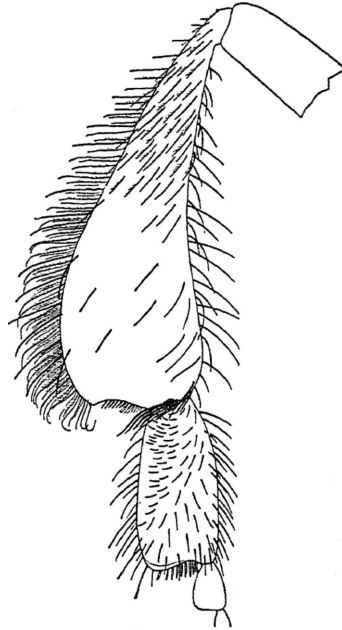


FIG. 48. Hind tibia and metatarsus of worker of *Trigona* (*Trigona*) *fulviventris* variety *fulviventris* Guérin. Drawing by Elena Feld.

tened over its basal three-fifths, rather strongly depressed over its apical two-fifths. The flattened area margining the under side of the hind tibiae posteriorly about one-third of the width of the joint towards the apex. The hind metatarsi a little more than one-half as wide as the hind tibiae at their widest, their apex posteriorly very slightly acute to almost rectangular. The hairs of the leg predominantly black except for the following: the plumose hairs intermixed with the black simple hairs on the external face of the middle tibiae a slightly diluted black; the microscopic but stubby hairs on the elevated part of the under side of the hind tibiae and adjacent apical part beneath of the hind femora

silvery gray; the metatarsal brushes with a copper sheen when viewed from certain angles but black when viewed from others; the suboval sericeous area at the base of the under side of the hind metatarsi also silvery gray to whitish but the coloration of its hairs often obscured by adherent foreign matter. The relative length of the hairs and their distribution as noted in the description of the worker of the subgenus *Trigona*.

WINGS: Subtransparent, with a much diluted yellow stain, the stain being of a uniform intensity throughout, not deeper in the basal region than in the apical. The veins and stigma ferruginous; the tegulae rufo-piceous to more or less black. The transverse cubital veins barely or not at all traceable. The first discoidal cell about three-fourths as long as the marginal. Number of hamuli per lower wing five, rarely six. Of 250 wings examined, 230 had five hamuli, and only 20 had six hamuli, an average of 5.08. The specimens from Córdoba, Mexico, showed a relatively greater number having six hamuli than those from other areas.

ABDOMEN: As a rule not greatly telescoped, of rather moderate length to sometimes elongate when the segments are exposed, narrower than the thorax, with its sixth and fifth tergites rather perpendicularly placed, and especially characterized among species of the subgenus *Trigona* in having in its typical form a fulvous to reddish abdomen combined with the dark head and thorax. The abdomen is not infrequently darkened somewhat on its apical tergites. The hairs black: a few semi-erect hairs over the apical one-half of tergite 3; the hairs longer on the exposed parts of the subsequent tergites. On the under side of the abdomen black erect hairs are present at the middle of the apex of each of the successive sternites and are flanked on sternites 3 to 5 by glistening, dense, silvery gray, sericeous patches.

MEASUREMENTS: Length 5 to 6.5 mm.; width of thorax 2 to 2.25 mm.; length of forewing, including tegula, about 7 to 7.5 mm.

QUEEN

Unknown.

MALE

HEAD: Black. The facial quadrangle much narrower than in the worker. The distance from one eye to the other at their level of closest approximation (below) a little more than four-sevenths of the length of the eye, whereas in the worker the shortest distance between the eyes is about four-fifths of the length of the eye. The clypeus and supra-clypeus a little more elevated than the sides of the face; the clypeus on the whole of even surface but inclined to be a little flattened medianly towards the apex; the apico-lateral angles of the clypeus approximately rectangular and in contact with the rim of the eye; the length of the clypeus about two-thirds its greatest width. The labrum very feebly bituberculate, much more feebly so than in the worker, the eminences barely detectable. The mandible somewhat thumb-shaped, its apical extremity bluntly pointed to narrowly subtruncate, edentate; the greater part of the mandible black but more or less reddish on approximately the apical one-fourth to one-third with the extreme apex in some cases narrowly darkened. The malar space virtually obsolete, the inner angle of the base of the mandible and the rim of the eye being in contact. The distance between the lateral ocelli distinctly greater than the distance between each lateral ocellus and the nearest compound eye, which is a trifle greater than the width of an ocellus; the ocelli larger than in the closely related *compressa*. The carina behind the ocelli more or less moderately developed. The silvery gray, appressed, microscopic hairs rather uniformly dense over clypeus, sides of face, front, and vertex and a little denser still over all but the lower extremity of the genal area. The erect hairs of the head black and somewhat scant, those of the clypeus usually a little longer than the rather sparse hairs of the front but distinctly shorter than the hairs of the vertex. The hairs of the scape are very short and fine, down-like rather than bristle-like, and usually wholly or largely pale. The dark hairs on the smooth lower extremity of the genal area and on the inferior edge of the mandibles moderately long but shorter than those of the vertex. The antennal sockets

pale ferruginous; the scape likewise pale ferruginous with a more or less extended dark stripe posteriorly; the flagellum dark above, light orange colored to brownish on the under side.

THORAX: Black. Silvery gray tomentose over all parts except the bare middle area of the propodeum, but with erect black hairs as well which in some of the specimens tend, however, to be sparse. The black hairs of the scutellum notably longer than those of the mesonotum.

LEGS: Black, here and there sometimes invaded by reddish brown, with the apical tarsal joint bright ferruginous. The hind tibiae narrow, almost straight (a little convex towards the apex) along their anterior lateral contour, somewhat convex along their posterior lateral contour; the posterior part of the outer face of these tibiae rather flattened and, towards the apex especially, somewhat concave; the contour of the apex of these tibiae rounded anteriorly, subtruncate posteriorly; the greatest width of these tibiae (near the apex) about two-thirds that of the conspecific worker at the corresponding level. The hind metatarsi only a little narrower than the associated tibiae, being fully three-fourths their width, the posterior apical extremity of these metatarsi subrectangular. The erect or for the most part semi-erect hairs predominantly black, those on the posterior face of the hind coxae very notably longer than those on the anterior face of the joint and conspicuously longer, too, than the hairs on the under side of any of the trochanters. In addition to the black hairs there are silvery gray, appressed, tomentose hairs on the outer face of the fore tibiae, such hairs still more abundant usually on the outer face and posterior lateral contour of the middle tibiae, and as a rule dense over the outer face of the hind tibiae; the plumose hairs along the posterior lateral contour of the hind tibiae very short and the simple black hairs intermixed with these hairs also at most of intermediate length. Also silvery gray are the hairs on the under side of the trochanters, the dense fringe of very microscopic hairs on the under side of the femora, the microscopic but stubby hairs down the raised area on the under side of the hind tibiae and on the ad-

jacent region and upward of the under side of the hind femora, and the area of appressed sericeous hairs at the base of the under side of the hind metatarsi. The metatarsal brushes deep copper color verging on black. The distribution of the simple black hairs generally and their relative length approximately as indicated in the generalized description of the male of subgenus *Trigona*.

WINGS: As described for the worker. Number of hamuli per lower wing five, more rarely six. Of 20 wings available for examination 17 had five hamuli and three had six hamuli, an average of 5.15.

ABDOMEN: Fulvous to ferruginous, and a little narrower than the thorax. Tergite 1 bare; tergites 2 and 3 virtually bare with at most a very few short hairs at the apex; tergites 4 to 6 with rather scant, erect, black hairs; tergite 7 fringed apically with such hairs. The sericeous hairs of the sternites silvery gray. For the structure of the sternites and genitalia, see figure 49.

MEASUREMENTS: Length 6 to 6.5 mm.; width of thorax 2 to 2.25 mm.; length of forewing, including tegula, about 6.5 mm.

TYPE MATERIAL

The material on which Guérin's description of *fulviventrís* was based came from Mexico.

DISCUSSION

It is possible that *fulviventrís* is merely a synonym of *ferruginea* Lepeletier. The description of *ferruginea*, so far as it goes, applies well to the insect Guérin subsequently described. Moreover the chances favor the presence of so abundant an insect among the 35 Meliponidae that Lepeletier named (1836, vol. 1, pp. 407-435). In the British Museum, specimens of the kind here designated *fulviventrís* have indeed been assigned to *ferruginea*. If I hesitate in accepting this interpretation, it is because the country where *ferruginea* was collected is unknown and the type is no longer in existence. Under these circumstances I do not feel justified in discarding a name so widely employed as *fulviventrís*.

As Cockerell has pointed out (1910c, p. 366), *laboriosa* F. Smith is a synonym of *fulviventrís*.

Ducke (1916, pp. 128-129; 1925, pp. 416-

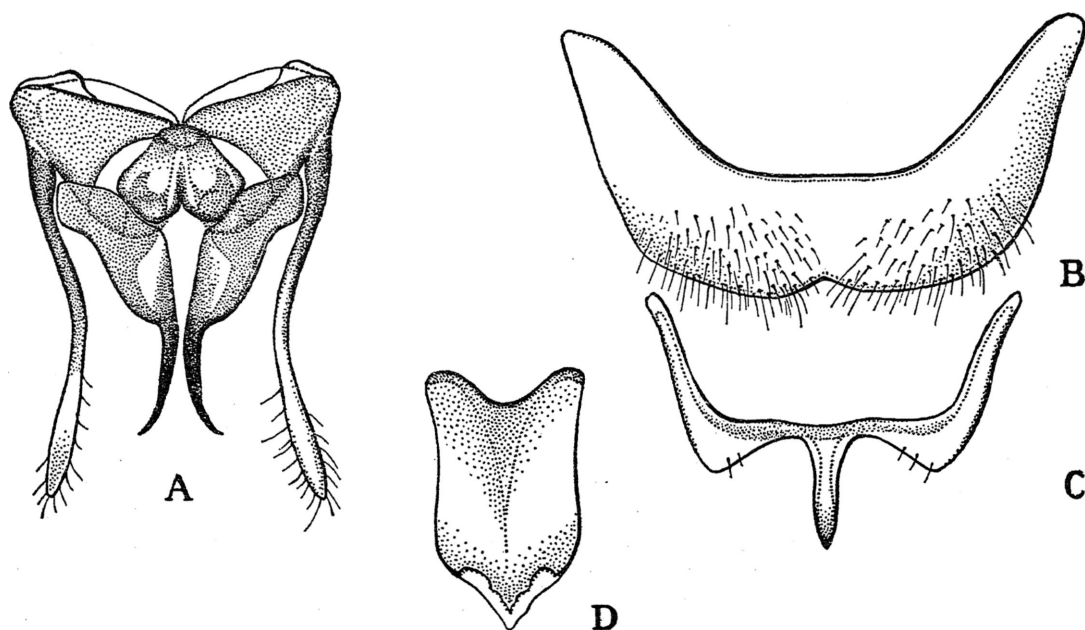


FIG. 49. Abdominal parts of male of *Trigona* (*Trigona*) *fulviventrís* variety *fulviventrís* Guérin. A. Genitalia (chitinized parts only). B. Sternite 5. C. Sternite 6. All based on a specimen from France Field, Canal Zone. D. Sternite 7, based on a specimen from Barro Colorado, Canal Zone. Drawings by Shirley H. Risser.

417; 1945, p. 97) ranks *fulviventrís* merely as an aberration of *argentata*. It would seem from this that Ducke interpreted *argentata* as the insect which Friese designated *Trigona fulviventrís* variety *nigra*¹ (see H. von Ihering, 1903, pp. 217–218) and which Cockerell (1910c, p. 366; 1912b, p. 61) described as *Trigona guianae* (here designated *fulviventrís* variety *guianae*). (For other interpretations of *argentata* the reader is referred to the discussion of *hypogaea*.)

Whether the *argentata* of Lepeletier be an insect structurally like *fulviventrís* or, as Friese has conceived it, equivalent to Silvestri's *hypogaea*, under neither interpretation is Ducke's assertion (1916, p. 129; 1925, p. 416) valid that, except for its darker color, *argentata* is just like *kohli*. Both *fulviventrís* and

its variety *guianae* are differentiated from *kohli*, which is a synonym of *pallida*, and indeed differentiated as well from all other *Trigona* of the subgenus *Trigona* except *compressa* and possibly *braueri*, in having a four-toothed mandible instead of a five-toothed mandible.

According to Gronen (1881b, p. 332; 1881c, p. 111), *fulviventrís* selects tree hollows as nest sites. The nests are frequently located close to the ground. Thus Marianno (1911, p. 98) noted no fewer than 11 colonies of this species in the Baixada of the Brazilian State of Rio de Janeiro that were established in the decayed roots of old trees. Lutz (1924b, p. 508) observed a nest in the Canal Zone that was founded in a hollow stump about 3 feet high. His field notes indicate that "the nest was built in among the fibrous roots." The nest in the "Allee tree" on Barro Colorado Island (pl. 1; fig. 2) is in the trunk of that tree—a sandbox—only about 2 feet above the soil. Of two nests noted by Michener (1946, p. 189) in Panama one was "at ground level at the base of a large buttressed tree" and the other "was about a foot above the ground

¹ Ducke (1925, p. 416), in commenting on the nest habits of his *argentata*, alludes to Friese's *Trigona fulviventrís* variety *nigra* as though it were a synonym. However, he also lists *hypogaea* Silvestri (the type of which he had apparently not seen) merely as an aberration or probable aberration of his interpretation of *argentata*. Silvestri's *hypogaea* is an insect very different from *fulviventrís*. It accords with the insect Friese interpreted as *argentata*, but not with what I believe to be Ducke's interpretation of *argentata*.

in a tree." Indeed, sometimes nests of *fulviventr* are actually erected in the ground itself. Thus near the Ancon-Panama City boundary, not a hundred yards from the Tivoli Hotel, Lutz (1924a, p. 213) found a nest located under the cement pavement, with the entrance to the nest at the edge of the cement. A nest figured by Rudow (1914, p. 241 and fig. 10) is plastered against the trunk of a tree, but possibly Rudow wrongly interpreted the species.

The nests of the closely related *fulviventr* variety *guianae* are apparently erected as a rule in termite nests established low in the trunks of trees. Thus H. von Ihering, after commenting on a colony of *guianae* that was founded in a nest of the ant genus *Camponotus*, stated that such an association must be considered exceptional, for he had been assured by one who had frequently observed nests of *guianae* that the bee always placed its colonies in the midst of a termite structure, either at the foot of the tree or at the beginning of its thick roots (1903, pp. 218-219). The fact that typical *fulviventr* in most of the instances recorded has its nests, like those of *guianae*, at the base of the trunk and even in the root system makes one wonder whether it, too, does not avail itself of termite structures so located. Indeed Wheeler (1923, p. 122) spoke of *fulviventr* as a species that builds "in the centers of termite nests."

In a field note attached to specimens of *fulviventr* sent me from Costa Rica by Mr. F. Nevermann, the observation is made that the combs are horizontal in arrangement and oval in shape "supported by columns of cerumen passing through." (See in this connection the citation from H. von Ihering about the supports in a nest of *fulviventr* variety *guianae*, p. 338.)

The subterranean nest observed by Lutz seemingly lacked an external entrance tube, but as a rule such a tube is provided. Marianno, writing from southern Brazil, asserted that the material used for the construction of the tube is almost exclusively fresh canine excrement and fragments of moss or other little-resistant vegetable substances. The nest in the "Allee tree" had a tube of irregular funnel shape. The orifice was elongate oval, about 4 inches in length by about 2 in width. The interior of the protruding tube

or funnel was beset with bees, mostly with their abdomen raised and facing outward. A *Trigona* of another species on one occasion attempted an entrance. My note regarding the occurrence reads: "A ball of two or three struggling bees disappeared into the interior" and it is to be assumed that the guarding bees had enveloped the intruder. "By 5:40 in the evening (Nov. 7, 1930) there were considerably fewer bees stationed on the inside of the trumpet, by 6 P.M. all were deep in the funnel and by 6:07 P.M. the retreat had been completed although there was at that time still enough light by which to read or write."

The records of flower visitations are more complete for *fulviventr* than for most stingless bees. Ducke (1902b, p. 313) concluded that it "visits every kind of bloom except Gramineae and Cyperaceae; it is the only bee for that matter which I regularly find visiting the scarlet and orange-red flowers of *Jacobinia*, *Pachystachys* and similar Acanthaceae, *Heliconia psittacorum* L. and related species, as well as *Passiflora coccinea*, all being plants especially sought out by humming birds." To this list Marianno (1911, p. 98) added the flowers of the banana. Mrs. T. D. A. Cockerell collected *fulviventr* on *Zexmenia virgulta*, *Ipomoea quinquefolia*, and *Pontederia cordata* (cited by Cockerell, 1912c, p. 314). Dr. Joseph Bequaert, who took this bee in Guatemala, has communicated to me the following observations: "*Trigona fulviventr* visits the flowers of *Melampodium divaricatum*.¹ It was also observed stealing honey from the flowers of the cultivated coffee through holes in the tube of the corolla, but it does not bite the holes, which are made by some other insect." In Guatemala, too, M. Bates observed it on conifer, and from the same state I have received a specimen from Dr. C. F. W. Muesebeck that was included among the visitors of *Cinchona*. In Mexico, A. Dampf saw it visiting a flowering agave.

Rau (1933, p. 27) noted *fulviventr* as one of the stingless bees attracted by the dung of the puma, and in Mexico A. Dampf collected it on the excrement of pigs. On the other hand, Ducke (1902b, p. 313) had never observed

¹ The plant was identified by Standley from specimens collected by Bequaert.

fulviventr visiting either carcasses or other rotting substances.

Fly traps baited with raw sugar proved attractive on successive days to *fulviventr* according to A. Dampf.

Mr. V. W. von Hagen, who collected this species in Montaña de la Flor-Orica, Department of Tegucigalpa, Honduras, has informed me that it is locally known as "puilu" by the Jicaques Indians, who have domesticated it. In southern Brazil it bears the name of "abelha de cachorro" (Marianno, 1911, p. 97; Ducke, 1916, p. 129; Ducke, 1945, p. 97).

In Honduras its wax is used for blowgun sights and for fixing arrows. The colonies of *fulviventr* are, however, less favored than those of *Melipona beecheii* Bennett, which are known by the natives under the name "tsaspena."

Marianno (1911, pp. 8, 53, 98) found *fulviventr* of southern Brazil timid and pacific, and the unaggressive behavior of this species has been noted also in the case of the colonies of its northern range.

According to H. von Ihering (1903, p. 218), the honey of the related *fulviventr* variety *guianae* has not a trace of aroma and is insipid in taste. On the other hand, Lutz (1924, p. 508) found the honey of typical *fulviventr* rather acid, while Gronen (1881b, p. 332; 1881c, p. 111) said it had the reputation in Colombia of being of good quality.

The presence of males in nest material is always of interest. Of more than 400 specimens of *fulviventr* obtained by F. E. Lutz at Colon on November 27, 1923, I found only a single male. The date in question is close to what is normally considered the end of the rainy season in the Canal Zone. Nest material consisting of 3039 specimens of *fulviventr* was kindly sent me by T. C. Schneirla from Huixtla, State of Chiapas, Mexico. In this aggregate there were 2748 workers, 290 males, and one physogastric queen. The specimens were collected on January 27, 1945, which falls within the dry season. On the other hand, males were present also in the two Panamanian colonies observed by Michener (1946, p. 190) respectively on February 22 and on July 23. On both occasions Michener noted assemblages of males consisting of 25 to 50 individuals. Of these only about

half were in flight at any given time. The others were sedentary on leaves, twigs, and tree trunks within 18 inches of the nest entrance.

DISTRIBUTION

The range of *Trigona fulviventr* extends from Mexico into Brazil. Cockerell (1920c, p. 461) expressed surprise that this insect was not represented in a collection from British Guiana that he had an opportunity to examine. I have myself failed to find it among material from British Guiana in the collections before me. So far as I am aware, *fulviventr* has not been reported from French Guiana. Among the collecting sites for *argentata* that Ducke (1916, p. 129; 1925, p. 417; 1945, p. 97) mentioned is Surinam, but it is not clear whether he intended to have this apply also to *fulviventr*, which he regards merely as an aberration of *argentata*. There are, at any rate, no specimens of *fulviventr* from Surinam in the collections here reported upon, although the form *guianae* is represented among the material from that country. All the Brazilian specimens before me are from the States of Pará and Ceará, but others (Marianno, 1911, p. 98, and Rudow, 1914, p. 241) have reported its presence far to the south in the States of Rio de Janeiro and São Paulo, respectively.

In the collections before me are specimens of *fulviventr* from the following states:

MEXICO: State of Vera Cruz: Orizaba, Jan. 9-16, 1892 (H. Osborn); Atoyac (Schumann); Córdoba (Crawford), June 13 (F. Knab), Nov. 20, 1924 (A. Dampf); Peña Blanca, near Córdoba, 1200 meters, Dec. 15, 1924 (A. Dampf); Jalapa (Crawford); Fortin de las Flores, Aug. 19, 1946 (H. F. Schwarz). State of Tabasco: Teapa, Jan. (H. H. Smith); between Tiradero and Pajarral Jan. 8, 1939 (A. Dampf). State of Campeche: La Lucha, Río Candelaria, Jan. 11, 1939 (A. Dampf); Candelaria, Nov., 1944 (M. Guerra). State of Yucatan: Valladolid (Gaumer); northern Yucatan (Gaumer); Chichen-Itza, June, 1929, male as well as worker, Aug. 28, 1946 (H. F. Schwarz). State of Chiapas: Belem, coffee plantation in Sierra Madre de Chiapas, 700 meters, June 24, 1935 (A. Dampf); Finca El Vergel, coffee plantation in Sierra Madre de Chiapas, near Huixtla, 700 meters, May 15, 1935, May 23-26, 1935, and May 26-June 3, 1935, in fly traps baited with raw sugar (A. Dampf); Finca Santa Julia, Sierra Madre del Sur, about 800 meters, Nov. 26,

1938, on a window pane (A. Dampf). State of Oaxaca: Yagalaxi, on excrement of pigs, Feb. 29, 1932 (A. Dampf). State of Guerrero: Amula, 6000 feet, Sept. (H. H. Smith); Acapulco (A. Agassiz), Sept. (H. H. Smith), Aug. 12, 1946 (H. F. Schwarz), and Acapulco Bay, Nov. 25-29, 1937 ("Zaca" Exped.); Rincon, 2800 feet, Sept. (H. H. Smith); Tierra Colorada, 2000 feet, Oct. (H. H. Smith); Acahuizotla, 3500 feet, Oct. (H. H. Smith); Hacienda de la Imagen, 4000 feet, Oct. (H. H. Smith); between Tixtla and Chilpancingo, 1700 meters, on flowering agave, Jan. 20, 1941 (A. Dampf). State of Colima: Colima, 400 meters, Feb., 1927 (R. Mueller); La Estancia, Oct., 1939 (A. Dampf). State of Jalisco: Tuxpan, Sept. 6, male (McClendon).

GUATEMALA: Guatemala City (Champion); S. Geronimo (Champion); Gualán, Jan. 12, 1905 (C. C. Deam); Polochic River, March 22 (Barber and Schwarz); Livingston, May 5-12 (Barber and Schwarz); Cacao, Trece Aguas, Department of Alta Vera Paz, Feb.-March, 1907 (G. P. Goll); San Cristobal (J. D. Norton); Chiquimulilla, 300 meters, Jan.-March, 1923 (Rene Lichy); Zacapa, Sept. 30, 1929 (M. Bates); Culpan, Jan. 28, 1930, on conifer (M. Bates); Las Sabanetas, Barberena, 1000 meters, Feb. 1, 1931 (J. Bequaert); Santa Emilia Pochuta, 1000 meters, Feb.-March, 1931 (J. Bequaert); Moca, Guatemala, 1000 meters, March-April, 1931 (J. Bequaert); Quiriguá (J. Bequaert); El Naranjo, Chicacao, July 7, 1945, on *Cinchona* (E. J. Hambleton); Puerto Barrios (E. Bethel); Coban.

BRITISH HONDURAS: Nov., 1928 (C. L. Lundell); Feb. 13, 1931 (W. Moore); Belize; Benque Viejo, male (Father Stanton).

HONDURAS: Tegucigalpa, Feb. 18, 1913, June 29, 1917, Aug. 1, 1917, Feb. 7, 1918 (F. J. Dyer); Monte Cristo, March 19-20 (W. M. Mann); Olanchito, April 24, 1923 (T. H. Hubbell); Tela, May 26, 1923 (T. H. Hubbell), (W. M. Mann); El Canal, Puerto Castilla, March 28, 1924 (J. Bequaert); Corocito, April 3, 1924 (J. Bequaert); Prieta, April 5-6, 1924 (J. Bequaert); Trujillo, Sept. 3 (J. Bird); Lancetilla, Aug. (R. E. Stadelmann); Subirana, Department of Yoro, Feb. 22, Feb. 26, 1933, March 12 (R. E. Stadelmann); Montaña de la Flor-Orica, Department of Tegucigalpa, 3200 feet, "pine-oak region," Dec. 30, 1937 (V. W. von Hagen), domesticated by Jicaques Indians.

EL SALVADOR: Sonsonate, Aug. 19 (F. Knab).

NICARAGUA: San Antonio, May, 1899; Chontales (Janson); San Marcos (Baker); Managua (Baker).

COSTA RICA: Cache (H. Rogers); Pozo Azul, June 15, 1902 (M. A. Carriker, Jr.); Pozo Azul de Perris, 325-350 feet, Aug. 19, 1927 (Lankester and

Rehn); Mt. Redondo, Jan., 1903; Suretka, April 26, 1924; Matina, Aug. 7 (A. Alfaro); Orotina, May 6-7, 1924; La Fuente, March 28, 1936 (A. Alfaro); Naranjo, April 29, 1937 (A. Alfaro), No. 171; Hamburg Farm, Nov. 27, 1937, Nest 31 (F. Nevermann); Port Parker, July 14, 1932 (M. Willocks, Jr., Templeton Crocker Exped.); San Mateo.

PANAMA: Porto Bello, Feb. 15, 1911 (A. Busck); Alhajuela, April 5-17, 1911 (A. Busck), Aug. 16, 1914 (T. Hallinan), May (A. H. Jennings); Cabina, May 27, 1911 (A. Busck); La Chorrera, April 12, 1912 (A. Busck); Las Sabanas, Nov. 17, 1923 (F. E. Lutz), and July 7, 1924 (N. Banks). Chiriqui Province: Bugaba (Champion); Volcan de Chiriqui, 2000-3000 feet (Champion), Feb. 18-29, 1936 (F. E. Lutz and W. J. Gertsch); Boquete, March 1-24, 1923 (F. M. Gaige); Progreso, April 14-21, 1923 (F. M. Gaige). Colon, Nov. 27, 1923 (F. E. Lutz), consisting of more than 400 workers but only a single male, all obtained from a "nest in hollow pine stump, stump about 3 feet high. Nest built in among the fibrous roots; flight hole inside; honey pots below. Bees gentle. Honey pleasant but rather sour"; Santa Rosa, Chagres River, March 13, 1933 (H. F. Schwarz); Potrerillos, May 8, 1935, May 11, 1935; Old Panama, Feb. 22, 1945 (C. D. Michener); Pueblo Nuevo, near Panama City, July 23, 1945 (C. D. Michener).

CANAL ZONE: Tabernilla, July 23, 1907, male (A. Busck); Paraiso, 1911 (A. Busck); Culebra, on Arraiján Trail, Nov. 27, 1914 (T. Hallinan); Gatun (A. H. Jennings); near Río Trinidad, Gatun Lake, March 25-27, 1920 (Cornell Univ. Exped.); Ancon, "nest under cement walk at foot of third post east of gate in fence along north side of main walk from Tivoli to railway station," Nov. 4, 1923 (F. E. Lutz) and June 18, 1924 (N. Banks); Frijoles, Nov. 8-15, 1923 (F. E. Lutz); Chiva Chiva Trail, Nov. 18, 1923 (F. E. Lutz); Barro Colorado Island, Nov. 11-13, 1923, males as well as workers (F. E. Lutz), June 23, 1924, and April 3, 1935 (W. M. Wheeler), June 20-23, 1924, and July 15-31, 1924 (N. Banks), Dec. 26, 1928-Jan. 10, 1929 (C. H. Curran), Nov. 11-Dec. 1, 1930 (H. F. Schwarz), March, 1933 (F. E. Lutz), March, 1933 (H. F. Schwarz), Feb. 9, 1936 (W. J. Gertsch); Fort Davis, July 5, 1924 (N. Banks), Feb. 9, 1929 (C. H. Curran); Mt. Hope, July 8, 1924 (N. Banks); France Field, Jan. 18, 1929, males (C. H. Curran).

COLOMBIA: Aracataca, Magdalena, Aug. 5, 1920; Hacienda Cincinnati, Sierra San Lorenzo, Magdalena, 4500 feet, July 17-19, 1920; Cartagena, Jan. 1, 1921 (E. W. Deming); Vista Nieva, 5000 feet, Santa Marta, Feb. 9-10, 1927 (G. Salt); Cerro Patron, 4000 feet, Río Frio, Magdalena, Aug. 1, 1927 (A. Schultze), Sept. 12, 1927 (G.

Salt); Puerto Colombia (P. T. Darlington); Muzo, 900 meters, Boyacá, June, 1936, males (J. Bequaert).

VENEZUELA: Lagunita de Aroa, 2000 feet, Dec., 1910 (M. A. Carriker); Aroa, on aster, Dec. 16, 1910 (M. A. Carriker).

BRAZIL: State of Pará: Pará, males as well as workers (C. F. Baker), May, 1901 (A. Ducke), July 13, 1924 (J. Bequaert); near Pará (N. B. Merrill); Igarapé-Assú, June 27, 1919, and July 15, 1919 (Parish); Prata, June 30, 1919, and July 9, 1919 (Parish). State of Ceará: Specimens lent by Cornell Univ.

Trigona (Trigona) fulviventrís variety
guianae Cockerell

? *Trigona argentata*, KRIECHBAUMER, 1900, p. 99.

Melipona argentata, DUCKE, 1902a, p. 420.

Melipona (Trigona) argentata, DUCKE, 1902b, p. 313.

Trigona fulviventrís var. *nigra* H. VON IHERING (nec *Trigona nigra* Cresson), 1903, pp. 185, 217-219, 244, 247, 257, 270, 279.

Trigona fulviventrís var. *nigra*, H. VON IHERING, 1904b, pp. 383, 386.

Trigona argentata, DUCKE, 1906a, p. 18.

Trigona guianae COCKERELL, 1910c, p. 366.

Trigona guianae, COCKERELL, 1912b, p. 61.

? *Trigona argentata*, WHEELER, 1913, p. 7.

Melipona argentata, DUCKE, 1916, p. 27, opposite p. 28, pp. 128-129.

Melipona argentata, BRËTHES, 1920, p. 53.

? *Trigona recursa* b, LUTZ, 1924a, pp. 205, 207, 210.

Melipona argentata, DUCKE, 1925, pp. 344, 346, 354, 416-417.

Trigona argentata, BISCHOFF, 1927, p. 289.

Trigona guianae, L. E. CHEESMAN, 1929, pp. 143, 149.

Melipona argentata, ALFKEN, 1930b, p. 2.

Trigona fulvicornis (sic) variety *nigra*, ALFKEN, 1930b, p. 2.

Melipona argentata, GUENTHER, 1931, p. 376.

Melipona argentata, ALFKEN, 1932b, p. 306.

Trigona argentata, MAIDL, 1934, pp. 164, 582.

Trigona (Trigona) fulviventrís variety *guianae*, SCHWARZ, 1938, pp. 438, 442, 454-455.

Melipona argentata, R. VON IHERING, 1940, p. 297.

Trigona (Trigona) fulviventrís variety *guianae*, SCHWARZ, 1940, p. 2.

Trigona fulviventrís guianae, MOURE, 1944a, p. 73.

Trigona (Trigona) fulviventrís guianae, MOURE, 1944b, p. 1.

Melipona argentata, DUCKE, 1945, p. 23, opposite p. 24, pp. 97-98.

WORKER

HEAD: As described for typical *fulviventrís* except that there is considerable variability in the coloration of the mandibles, which are in many cases largely red, as are those of the typical form, and in other instances more or less cloudy, reaching the extreme in certain specimens (see discussion) that have the mandibles entirely black except for a red band just before the apex. Specimens thus distinguished also sometimes have the labrum black instead of red.

THORAX: As described for typical *fulviventrís*.

LEGS: As described for typical *fulviventrís*.

WINGS: As described for typical *fulviventrís* or now and then a little darker. Number of hamuli per lower wing usually five, more rarely six, very rarely seven. Of 154 wings examined 134 had five hamuli, 19 had six hamuli, one had seven, an average of 5.14.

ABDOMEN: Differs from that of typical *fulviventrís* in being black or blackish instead of fulvous.

MEASUREMENTS: Length 5 to 6.5 mm.; width of thorax 2 to 2.25 mm.; length of forewing, including tegula, 6.5 to 7.5 mm.

QUEEN

Unknown.

MALE

HEAD: As described for typical *fulviventrís*.

THORAX: As described for typical *fulviventrís*.

LEGS: As described for typical *fulviventrís*.

WINGS: As described for typical *fulviventrís*. Number of hamuli per lower wing usually five, rarely four or six. Of 32 wings available for examination, 28 had five hamuli, three had four hamuli, and one had six hamuli, an average of 4.94.

ABDOMEN: Differs from that of typical *fulviventrís* in being black or blackish instead of fulvous. For the variability in the structure of sternites 6 and 7, see figure 50.

TYPE MATERIAL

The type, from Guiana, is in the British Museum (Natural History).

DISCUSSION

There is considerable range of variation in the coloration of the mandibles of *guianae*. The type, from Guiana, had "dark reddish mandibles." Some of the specimens before me, including a number from British Guiana, have mandibles that resemble those of typical *fulviventr* in being red except for the black apical teeth and black basal prominences. Others have mandibles that are more or less cloudy red. From the latter condition it is

the conformation of the apex of the joint in question.

Under the designation of *fulviventr* variety *nigra* an informing account of the nest of *guianae* is presented by H. von Ihering (1903, pp. 217-219). Von Ihering was able to examine two nests of this bee. One of these was located in a termite nest that had been constructed in the hollowed base of a Tapiá trunk, with the excavated part occupied by the insect tenants extending into the thickest of the roots. The other nest was located in the

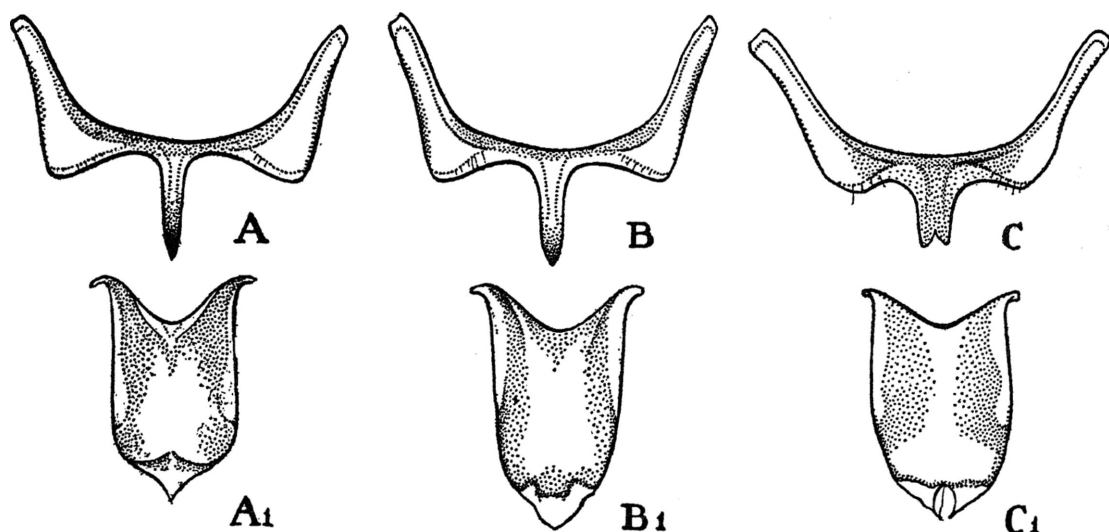


FIG. 50. Variability shown by *Trigona (Trigona) fulviventr* variety *guianae* Cockerell. A, A1. Sternites 6 and 7, respectively, of a specimen from Gorgona Island. B, and C. Sternite 6, and (B1 and C1) Sternite 7, of two specimens, both from Kartabo, British Guiana. Drawings by Shirley H. Risser.

only a slight transition to the specimens that have completely black mandibles except for a red stripe behind the apex. This dark extreme is very prevalent and occurs widely, if interruptedly, over the known range of *guianae*. Virtually all of the specimens I have seen from Peru have the predominantly black mandible, and specimens from this state are also apt to evidence a slightly darker tinge in the wing. The percentage of specimens having six hamuli instead of five is particularly large in the case of the Peruvian examples.

The original description of *guianae* speaks of the apex of the hind tibiae as "broadly truncate," which is suggestive of a condition like that in *nigerrima*, but I think the description here given more accurately indicates

interior of an ants' nest (*Camponotus* species) that entirely filled a spacious hollow in the base of a *Sapopema* tree. The hollow was nearly 1 meter in diameter and penetrated in part the roots. The bee nest was surrounded on all sides by the nest mass of the ants. It is to be noted that both of these nests, as with most of the reported nests of typical *fulviventr*, were located at the very base of their respective trees in a hollow that penetrated even the roots, but it is of special interest that in this location they were built into the structures of other insects. The association of stingless bees with termites is not uncommon, and von Ihering indicated (pp. 218-219) that in southern Brazil at least it is the almost invariable nest site of the dark variety of *fulvi-*

ventris. The instance of a *fulviventr* nest in the very heart of an ant nest is far more unusual.¹

Von Ihering devoted a more detailed description to the nest in the interior of the termite structure (which completely enveloped it) than he did to the nest located in the structure of the ants, but the latter was "in its arrangement essentially like" the former. Of the nest in the interior of the termite structure he says:

"In certain parts of the nest the net-work of the termite structure is firmly combined with the bees' nest, . . . especially toward the upper narrowed end. The latter was prolonged upward as a tube about 6 cm. wide and 60 cm. in length that reached the exterior of the trunk at a height of 60 to 70 cm. above the level of the earth and expanded at the entrance hole into a short wide funnel protruding from the trunk.

"The tube just mentioned as well as the firm outer shell that surrounded the entire nest, consisted of a compact and very hard mass of blackish-brown color, which when burned in a flame, left an inconsiderable charred residue, and accordingly did not consist of wax.

"The larger part of the nest was occupied—and this applied especially to the lower half—by the brood mass. The entire nest . . . is 52 cm. long and 25 cm. wide. The brood mass consisted of 25 combs of a diameter of 22 cm. The individual cells are 6 mm. long, 4 mm. high, the space between the individual combs is 4 to 5 mm. Very peculiar and differing radically from the generally observed condition of *Trigona* nests is the manner in which the individual brood-combs are fastened to one another. Whereas this is accomplished in other instances through short wax-pillars which extend from one comb to another, there are present in the nest here discussed long cables consisting of the same hard material of which the outer shell is composed. These uniting cables are seen at the periphery of the brood combs as well as in the inner part of these, which they often penetrate for considerable distances. In some places one can trace these cables over eight

to 10 combs; in most cases, however, they terminate dichotomously or in a branching manner. Thus there comes into being a ramified system of solid beams, which lends the colossal brood-cluster the necessary support. The individual cables are 3 to 4 mm. thick, but some of them may be as much as 8 mm. in thickness.

"In the upper half of the nest was noticed a second entrance hole, 30 mm. wide, 14 mm. high, which merged into another passageway that presumably joined the main tube. The upper part of the nest was in the main occupied by honey-pots although closer to the brood-cluster there were also scattered pots with pollen. The honey-pots are exceedingly numerous but very small. They are for the most part 10 mm. long and 6 mm. wide, but there are some the shape of which is approximately round."

The royal cells, 11 by 6 mm., were, as usual, on the periphery of the combs, and the large population of the nest, which was collected on October 19, 1900, included males.

On Gorgona Island L. E. Cheesman (1929, p. 149) observed a nest of *guianae* in "a living tree-trunk," but the height of the nest above the ground is not indicated. Cheesman gave these interesting facts regarding the external architecture of the nest and the uses to which the resin is put: The nest had "a cerumen spout entrance 5½ inches in length, 2¼ inches wide, flattened dorsally. It was constructed with fragments of bark worked into the material so that it had the appearance of a broken branch. Colombian natives from the mainland informed me that they are in the habit of taking the nests of this species for the sake of the resinous material stored by the bees, described as being present in large, yellow lumps, which the fishermen use for caulking leaking canoes."

In one of his early papers Ducke (1902a, p. 420; 1902b, p. 313) believed the form of dark abdomen (*guianae*) specifically distinct from *fulviventr*, basing this conclusion, however, not on structural grounds but on the divergent behavior of these two bees. Of *guianae* he noted that it was "rarely on flowers, mostly on rotting substances, excrement, and the like," and added that, when he worked at the Goeldi Museum, specimens of *guianae* visited often in great

¹ See Introduction (pp. 15-16) and also discussion of *Trigona* subgenus *Paratrigona* (pp. 352-353) for other instances of stingless bees established in ant nests.

numbers the flesh of dead animals that were to be mounted as museum exhibits. Very close to the quarters of the preparator were a number of banana plants that always bore more or less bloom. Yet never did Ducke detect even a single specimen of *guianae* on these flowers, whereas *fulviventr*is flew to them in multitudes. On the other hand, Ducke did not note *fulviventr*is visiting carcasses. It is possible, however, that Ducke in recording these habits confused the present species with *hypogea* (see discussion of *hypogea*, p. 232, footnote), which is distinctly partial to decaying flesh and which figures in his synonymy of *argentata* (= *guianae*).

L. E. Cheesman (1929, p. 143) on the other hand, recorded *guianae* as visiting one of the Compositae on Gorgona Island, Colombia.

"Mel de cachorro" is the popular designation for this bee in southern Brazil (H. von Ihering, 1903, p. 217; 1904b, p. 386), a name which it has acquired because of the poor quality of its honey. As H. von Ihering (1903, p. 270) pointed out, "mel de cachorro" means "dogs' honey."

The bee is not aggressive.

DISTRIBUTION

According to Ducke (1925, p. 417), the range of the insect which he interprets as *argentata* is from the tropical part of Mexico to tropical southern Brazil. But he does not indicate whether the range of the dark-bellied form (here designated *guianae*) of his *argentata* is coextensive with that of the fulvous-bellied form *fulviventr*is. Although the specimens before me indicate in the case of *fulviventr*is a range extending from Mexico into Brazil, the specimens of *guianae* here reported upon include no specimens from Central America. By way of compensation three countries of South America (Ecuador, Peru, and Bolivia) from which there is no typical *fulviventr*is are represented by specimens of *guianae*, and similarly the south Brazilian states, which in the collections before me likewise have no representatives of typical *fulviventr*is, offer a number of examples of the dark variety. It would seem likely, therefore, that *guianae* is the predominant form in South America and *fulviventr*is possibly the exclusive form in Central America and Mexico.

Trigona guianae was described by Cockerell from Guiana, and subsequently (1912b, p. 61) he recorded its presence also at Porto Velho in the State of Amazonas, Brazil.

In the collections here reported upon there are specimens from the following localities:

COLOMBIA: Without designation of locality (Harry Sargent). Gorgona Island, 02°59' N., 78° 20' W., July 1924, males as well as workers (L. E. Cheesman).

VENEZUELA: Barinas (P. J. Anduze); Barinitas (P. J. Anduze); Mt. Duida region, Nov. 4, 1928 (G. H. H. Tate).

SURINAM: Kwakoeegron, Saramacca River, June 8-11, 1927 (Cornell Univ. Exped.); Zanderij Island, Boven, Para District, April 22, 1927 (Cornell Univ. Exped.).

BRITISH GUIANA: Bartica, April 16, 1913 (Cornell Univ. Exped.); Bartica District, March 13, 1924, males, April 12, 1924, males (W. Beebe); Turesi Fall, Oct. 12, 1922; Kartabo, Aug. 9, 1920 (W. M. Wheeler), June and Sept., 1922 (M. D. Haviland), July 24, 1924, males, July 22, 1924, and Aug. 1, 1924, males (J. F. W. Pearson); Matope, July 23, 1924 (J. F. W. Pearson); Camaria, July 31, 1924 (J. F. W. Pearson); Kalacoon, June 15, 1926 (J. F. W. Pearson); Kamakusa, Jan., 1923 (H. Lang); Tumatumari, May 23, 1929 (A. Mackie); Amatuk, May 24, 1929 (J. Ogilvie); Kaieteur, May 26-27, 1929 (A. Mackie); Wanaina, Northwest District, March, 1931 (J. G. Myers); Moraballi Creek, Essequibo River, Aug. 25, 1929 (Oxford Univ. Exped.); Monkey Jump, Essequibo River, Oct. 7, 1929 (Oxford Univ. Exped.); Forest Settlement, Mazaruni River, Aug.-Sept., 1935 (N. A. Weber); Aracara Cataract to Popikai Falls, Mazaruni River, Aug. 14, 1920, No. 625 (R. E. Wheeler); upper Essequibo River, Dec. 23, 1937 (W. G. Hassler); Paruiama Mission, Kamarang River, upper Mazaruni District, Oct. 6, 1938 (A. A. Pinkus).

BRAZIL: State of Amazonas: Itacoatiara, Nov. 22, 1919 (H. Parish); Tefé, Feb. 5, 1920 (H. Parish); Esperanza, Aug. 9, 1920 (Cornell Univ. Exped.); Flores, July 29, 1924 (J. Bequaert); Manáos (H. B. Merrill). State of Pará: Santarem (H. H. Smith); Prata, July 31, 1919 (H. Parish); Pará, Aug. 30, 1919; Furo de Ressaco, Rio Amazonas, Sept. 10, 1920, at night (Cornell Univ. Exped.). State of São Paulo: Ypiranga; Alto da Serra, March 12-16, 1912 (G. E. Bryant). State of Rio de Janeiro: Tijuca, Oct. 17, 1919 (Cornell Univ. Exped.); Alta Boa Vista, Oct. 30, 1919 (Cornell Univ. Exped.); Rio de Janeiro, Nov., Dec., 1926 (A. Seitz); Itatiaya, Feb. 4-8, 1927 (A. Seitz). State of Matto Grosso: Chapada (probably Sant' Anna do Chapada, near Cuyabá).

PERU: Río Charapa, Sept. 12, 1911 (C. H. T. Townsend); El Campamento, Colony of the Perené, June 19–21, 1920 (Cornell Univ. Exped.); beyond Azupizú, July 9, 1920; Iquitos, July 28, 1920 (Cornell Univ. Exped.), and March 18, 1924 (H. Bassler); middle Río Marañón, Nov. 5, 1924 (H. Bassler); Puerto Alfonso, Río Putumayo, Aug. 14, 1920 (Cornell Univ. Exped.); Chanchamayo (Rosenberg); Tingo Maria, Río Huallaga, 700 meters, April, 1940 (W. Weyrauch).

BOLIVIA: Covendo, Sept. (W. M. Mann).

ECUADOR: Tena, March 4, 1923 (F. X. Williams); Abitagua, Oriente, 1200 meters (W. Clarke-MacIntyre); Río Pastaza, March 19, 1939 (F. M. Brown).

Trigona (Trigona) compressa Latreille

Trigona compressa LATREILLE, "1811"b, p. 294, pl. 20, fig. 7.

Trigona compressa, PERTY, [1833], p. 26.

Melipona compressa, DALLA TORRE, 1896, p. 577.

Trigona lacteipennis FRIESE, 1900a, p. 385.

Melipona hyalinata, DUCKE, 1901, pp. 31, 64.

Melipona lacteipennis, DUCKE, 1902a, pp. 323, 419.

Melipona (Trigona) lactipennis (sic), DUCKE, 1902b, pp. 292, 315.

Trigona lacteipennis, SCHULZ, 1904b, p. 828.

Trigona lacteipennis, SCHULZ, 1905c, p. 138.

Trigona compressa, DUCKE, 1910b, p. 368.

Trigona lactipennis, MARIANNO, 1911, p. 113.

Trigona pellucida COCKERELL, 1912b, p. 50.

Melipona compressa, DUCKE, 1916, p. 14, opposite p. 28, pp. 31, 75–77, pl. 5, fig. 16.

Melipona compressa, DUCKE, 1925, pp. 343, 351, 386–388, text fig. Q, pl. 4, fig. 13.

Melipona compressa, ALFKEN, 1930b, pp. 2, 9.

Trigona compressa, SCHWARZ, 1934, p. 3.

Trigona (Trigona) compressa, SCHWARZ, 1938, pp. 442, 452–454.

Trigona compressa, SNODGRASS, 1941, p. 61, pl. 30, figs. N, O.

Trigona compressa, MOURE, 1944a, p. 73.

Melipona compressa, DUCKE, 1945, p. 13, opposite p. 24, pp. 27, 59–61, pl. 5, fig. 16.

WORKER

DIAGNOSTIC CHARACTERS: Black. Mandible four toothed, the fourth and innermost tooth obsolescent, black except for a reddish stripe near the apex. Length of malar space about equal to width of flagellum. Clypeus smooth and even, without a fossa bisecting it and not apically foveate, its length somewhat less than half its greatest width. The erect black hairs on clypeus and supraclypeus

very short, barely longer than most of those on the scape. Labrum simple. Hind tibiae with an inwardly placed angle posteriorly at the apex; the outer face of these tibiae rather strongly depressed over the apical two-fifths. Wings predominantly milky white, the median cell sometimes darkened. Almost invariably characterized by its very narrow, dorsally ridged, laterally compressed abdomen.

HEAD: Black or mainly black. The facial quadrangle rather wide, the distance between the compound eyes at a level just below the anterior ocellus about equal to the distance between the anterior ocellus and the apex of the clypeus. The compound eyes rather strongly convergent below, the distance that separates them at their level of greatest approximation (below) about as 6.75 to 8 when compared with their divergence at the level just below the anterior ocellus. The clypeus raised a little above the level of the sides of the face, of smooth and even surface, without a median fossa and not foveate apically; its



FIG. 51. Mandible of worker of *Trigona (Trigona) compressa* Latreille. Drawing by Alice Gray.

width, measured from one apico-lateral extremity to the other, a little more than twice its length; each anterolateral extremity of the clypeus separated from the nearest compound eye by less than the width of the flagellum. The supraclypeus no more prominent than the clypeus. The labrum simple, without a trace of tubercles, its apex subtruncate. The mandibles (fig. 51) quadridentate along the apex. A thin septum of chitin sometimes between the two outermost teeth; the third tooth narrowly separated from the second by the intervening nick; the fourth tooth obsolescent, sometimes little more than the inner angle of the mandible and widely separated from the third tooth by an emargination that is shallower than is the case in the mandible of *fulviventrís* and its

variety *guianae*. The malar space, measured from the lower extremity of the eye to the middle of the base of the mandible, about equal to the width of the flagellum. The distance between the lateral ocelli a trifle less than that which separates each lateral ocellus from the nearest compound eye. The carina behind the ocelli rather feeble. The occipital contour very strongly concave. Fine, appressed, silvery gray, microscopic hairs of considerable density on the sides of the face and also present to some extent on the clypeus, but sparse to absent on the front and vertex; the genal area silvery gray pruinose (sometimes olivaceous viewed from certain angles). The erect hairs of the head black (except those fringing the mandibles below, which tend to be copper colored), abundant but short: those on the clypeus and supra-clypeus rather uniform in length and barely longer than the great majority of those on the scape, which tend to be shorter than the scape is wide; the hairs on the front dense and longer, although at best only of moderate length. The hairs on the vertex, mandibles below, and lower one-third of genal area among the longer hairs of the head. A few fairly long hairs on the labrum, and minute erect black hairs sparsely present among the silvery gray appressed hairs on the sides of the face and on the upper two-thirds of the genal area, these hairs occurring especially in the areas close to the orbits of the eye. Although devoid of true punctation, the chitin of the front is sometimes a little granular at the points of emergence of the hairs. The clypeus and labrum in fully developed specimens black; in callow specimens more or less suffused with reddish brown. The mandibles black except for a reddish or brownish area near the apex, just basad of the black apical teeth. The scape and flagellum black, usually wholly so, the under side of the flagellum being rarely differentiated strongly from the upper (only in the specimens from Chapada among those here reported upon is the under side of the flagellum distinctly ferruginous).

THORAX: Black or blackish, its sides sometimes more or less suffused with reddish brown. The mesonotum, scutellum, pleura, and sides of propodeum with their sheen subdued by the presence over these parts of

rather dense dull gray tomentum that in some lights seems brownish, especially that on the mesonotum. The erect hairs in these parts black, those on the mesonotum short, the others relatively longer as indicated in the description of the subgenus *Trigona*.

LEGS: Black, now and then invaded slightly by brownish; the apical joint of the tarsi frequently more or less reddish but in other cases black. The hind tibiae (fig. 52)

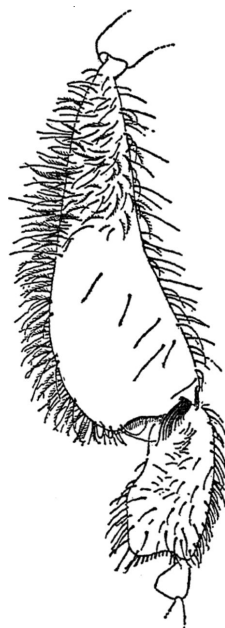


FIG. 52. Hind tibia and metatarsus of worker of *Trigona (Trigona) compressa* Latreille. Drawing by Alice Gray.

clavate in outline, considerably wider at the apex than at the base; their anterior lateral contour feebly emarginate; their posterior lateral contour strongly convex; their apex with an inconspicuous angle anteriorly that bears the tibial comb; beyond this angle there is a slight bulge in the apical contour followed by an emargination that results in a somewhat inwardly placed angle where this emargination encounters the posterior lateral contour. The outer face of the hind tibiae very gently arched to almost flattened over its basal three-fifths, rather strongly depressed over its apical two-fifths. The flattened area margining the under side of the hind tibiae posteriorly about one-third of the

width of the joint towards the apex. The hind metatarsi a little more than half the width of the hind tibiae at their widest; the posterior apical angle subrectangular to very slightly acute. The hairs of the leg black except for the following: sometimes the plumose hairs intermixed with the black simple hairs on the outer face of the middle tibiae, and even those on the outer face of the hind tibiae are gray rather than black; the microscopic but stubby hairs on the elevated part of the under side of the hind tibiae and adjacent apical part beneath of the hind femora are silvery gray, as is likewise the sericeous suboval patch at the base of the inner face of the hind metatarsi when not discolored by adherent foreign matter. The relative length of the hairs and their distribution as noted in the description of the worker of the subgenus *Trigona*.

WINGS: With the median cell sometimes a little darkened, rarely strongly so, owing to the presence in such cases of microscopic blackish hairs, but the rest of the wing as a rule more or less milk white. The bright ferruginous stigma and the concolorous veins of the apical part of the wing usually somewhat contrasted with the frequently darkened costal and subcostal veins. The transverse cubital veins barely or not at all traceable. The first discoidal cell virtually the same length as the marginal cell. Number of hamuli on each hind wing usually five. Of 93 wings examined 92 had five hamuli and one had four hamuli, an average of 4.99.

ABDOMEN: More or less compressed laterally, with the result that the tergites slant, roof-like, downward on each side of a median longitudinal dorsal carina, the shape of the abdomen being in consequence more or less quadrate or cylindrical or even wafer-like in shape, and always very conspicuously narrow when compared with the thorax. The abdomen black or blackish, usually much elongated, with in most cases all its segments rather fully revealed. The first four tergites virtually glabrous: only a thin representation of very fine microscopic appressed hairs traceable with difficulty along the apex of tergites 2 to 4 and sometimes indeed missing; tergite 4, in addition, with sometimes a few ultra-stunted black hairs. The hairs along the apex of tergite 5 semi-erect, short, and coarse,

not conspicuous. The black hairs on tergite 6 longer, much denser, and coarse, well covering the tergite. The ventral segments with erect black hairs arranged along the middle of the apical one-half of each; sternites 3 to 5, in addition, with a dense glistening brownish to silvery gray sericeous patch at each side of the area covered by the erect hairs.

MEASUREMENTS: Length 5.5 to 6.75 mm. (due largely to the distention of the abdomen); width of thorax about 1.75 mm.; length of forewing, including tegula, about 6.25 mm.

QUEEN

Unknown.

MALE

HEAD: Black. The facial quadrangle much narrower than in the worker. The distance from one eye to the other at their level of closest approximation (below) a little more than four-sevenths of the length of the eye, whereas in the worker the shortest distance between the eyes is almost equal to the length of the eye. The clypeus and supra-clypeus a little more elevated than the sides of the face, on the whole of even surface but inclined to be somewhat flattened to subfoveate apically at the middle; the apicolateral angles of the clypeus approximately rectangular and in contact or almost in contact with the rim of the eye; the length of the clypeus about two-thirds its greatest width. The labrum simple. The mandible somewhat thumb shaped, its apical extremity bluntly pointed to narrowly subtruncate, edentate; the mandible virtually all black, with at most only a narrow and indistinct stripe of red immediately behind the apex. The malar space reduced to the vanishing point, the basal inner angle of the mandible being in contact with the rim of the eye. The distance between the lateral ocelli greater but not much greater than that between each lateral ocellus and the nearest compound eye, which approximates twice the diameter of an ocellus; the ocelli smaller than in the closely related *fulviventr*. The carina behind the ocelli rather feeble. The silvery gray, appressed, microscopic hairs on the clypeus and sides of face usually not especially conspicuous, while

those of the front are frequently even less so, the similar silvery gray appressed hairs over all but the lower extremity of the genal area usually somewhat more lustrous. The erect hairs black, those of the clypeus rather short but longer than the very short black hairs on the scape and of comparable length with the black hairs on the front while shorter than those of the vertex; the hairs fringing the mandibles below (especially towards the

hind tibiae narrow, almost straight (a little convex towards the apex) along their anterior lateral contour, somewhat convex along their posterior lateral contour; the posterior part of the outer face flattened and at the apex a little concave; the apical contour rather uniformly rounded posteriorly as well as anteriorly; the greatest width of these tibiae (near the apex) a little more than two-thirds the width of the hind tibiae of the

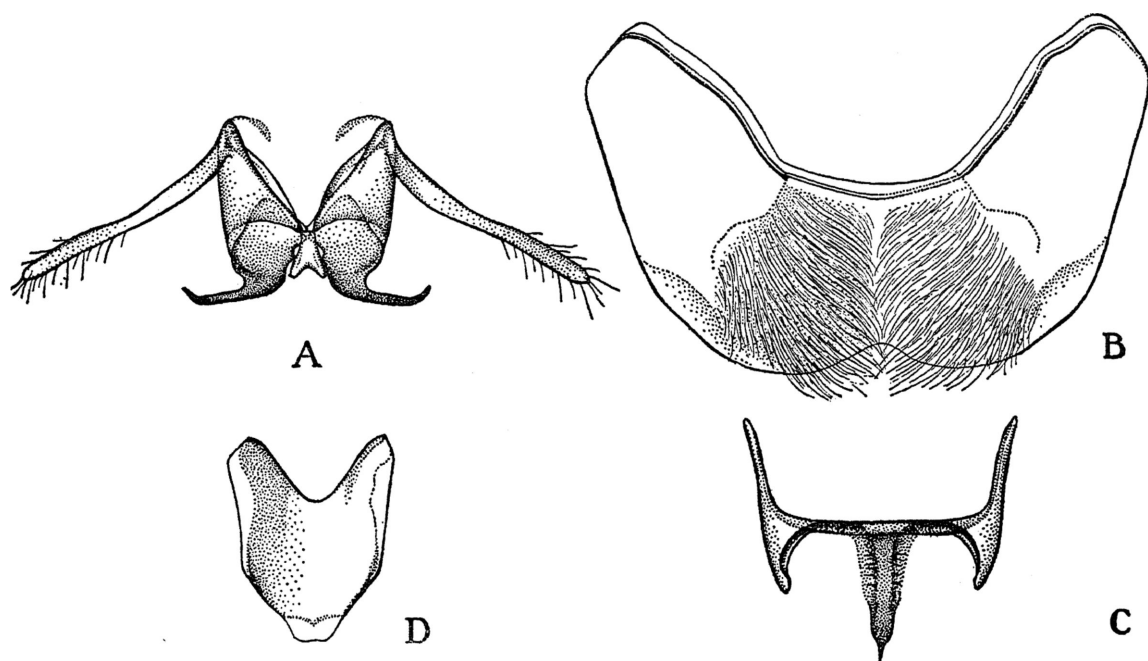


FIG. 53. Abdominal parts of male of *Trigona (Trigona) compressa* Latreille. A. Genitalia. B. Sternite 5. C. Sternite 6. D. Sternite 7. All based on a specimen from Bartica, British Guiana. Drawings by Shirley H. Risser.

base) and the hairs towards the lower extremity of the genal area also relatively long. The scape black and the flagellum also mainly dark with its under side only a very little lighter, if at all, than the black upper side.

THORAX: Black, of subdued sheen, especially on the mesonotum, due to the presence of grayish to darker tomentum over all parts except the bare middle area of the propodeum. The erect hairs black, moderately dense, much shorter on the mesonotum than on the scutellum or mesopleura.

LEGS: Dark except for the tarsal joints, especially the ferruginous apical one. The

worker at the corresponding level. The hind metatarsi only a little narrower than the associated tibiae, being fully three-fourths their width, the posterior apical extremity of these metatarsi subrectangular to rounded. The erect or for the most part semi-erect hairs predominantly black, those on the posterior face of the hind coxae notably longer than those on the anterior face of the joint and longer, too, than the simple hairs (which tend to be black) on the under side of the trochanters; the tomentum of the under side of the trochanters more or less grayish. In addition to the black hairs there are dull gray plumose hairs rather abundant usually on the

outer face and posterior lateral contour of the middle tibiae and of the hind tibiae. More or less silvery gray are the dense fringe of very microscopic hairs on the under side of the femora, the microscopic but stubby hairs down the raised area on the under side of the hind tibiae and on the adjacent region and upward of the under side of the hind femora, and the area of appressed sericeous hairs at the base of the under side of the hind metatarsi. The metatarsal brushes deep copper color to black. The distribution of the simple black hairs and their relative length approximately as indicated in the generalized description of the male of subgenus *Trigona*.

WINGS: As described for the worker. Of the 280 lower wings examined, 212 had five hamuli, 65 had six hamuli, and three had seven hamuli, an average of 5.25.

ABDOMEN: Black, laterally compressed, dorsally carinate, very narrow (much narrower than the thorax), and usually long as in the worker, shiny and in large part bare, with tergite 1 wholly bare, tergites 2 and 3 bare except for an inconspicuous narrow area along the apex where very microscopic appressed dark hairs are traceable. The tergites apical of tergite 3 with similar but larger apical bands of appressed, rather sericeous, grayish to blackish hairs (all of the exposed part of the tergites being usually covered with such hairs) but with few or no erect hairs. Tergite 7 fringed apically with short dark hairs. The sericeous hairs of the sternites grayish to brownish. For the structure of the sternites and genitalia, see figure 53.

MEASUREMENTS: Length 5.5 to 6.25 mm.; width of thorax 1.75 to 2 mm.; length of forewing, including tegula, 6 to 6.25 mm.

TYPE MATERIAL

The type, from Brazil, seems to be no longer in existence. The type of *pellucida* was generously donated to the American Museum of Natural History by Professor Cockerell.

DISCUSSION

Ducke (1925, p. 351) placed *compressa* in his Group III, on the basis apparently of its compressed abdomen, for he indicated as characteristic of his Group III a broad head and narrow abdomen. Nevertheless, in the case of *compressa* it is doubtful whether the

abdomen is as trustworthy a guide to the relationship of the insect as are the structure of its mandibles and its hind legs. My own belief is that the closest relative of *compressa* is *Trigona fulviventrís*, especially the black-bellied form (variety *guianae*), which it resembles in many respects. The fact that the mandibles of *compressa* are fully toothed¹ (although the dentition is sometimes obscured by thin septa of chitin between the teeth), the further fact that the hind tibiae are posteriorly fringed by branched hairs, and that on the under side of the hind metatarsi there is near the base an oval patch that is sericeous in striking contrast to the erect, stiff, tarsal brushes on the rest of the under surface of this joint all convince me that *compressa* belongs in what is here designated *Trigona* subgenus *Trigona*, most of the other representatives of which appear in Ducke's Group V.

Ducke (1925, p. 388) stated that *compressa* "mimics frequently in its coloration *dimidiata*, but is much smaller; its strongly compressed abdomen is also an arresting character." By coloration Ducke undoubtedly means the coloration of the wings, as the black body of *compressa* is shared by many other *Trigona*. Latreille himself ("1811" b, p. 294) in describing *compressa* had alluded to the "blackish base" of the wings, and this is the condition likewise of certain specimens from French Guiana in the museum in Paris. Specimens in the collections before me have wings of the somewhat milky hue to which Friese gave recognition when he named the insect *lacteipennis*. None of them, however, have the basal third of the wing stained a deep brown as in *dimidiata*; at most they are a little darker in the median cell, owing to the presence of microscopic dark hairs in this cell. The venation of the basal third or half of the wing is, however, apt to be dark in contrast to the bright ferruginous stigma and the equally bright ferruginous veins of the apical part of the wing. Cockerell's *pellucida* differs from the more usual condition in *compressa* in that the veins of the basal third of its wings are ferruginous as are those of the apical two-thirds.

¹ The dentition, although quadridentate, occupies the apex of the mandibles from end to end.

While in all specimens of *compressa* the abdomen has a dorsal carina, the degree of compression differs even among specimens of a single series. Usually the abdomen is decidedly elongate, considerably longer than the head and thorax combined. In the series from the Mt. Duida region, however, the abdomen is in most of the specimens exceptionally foreshortened, although one or two of the specimens in the series from that region have the more usual appearance. The telescoping or the extension of the segments of the abdomen has, of course, little diagnostic significance, but as *compressa* can usually be separated from its relatives even by the unaided eye because of the elongate and flattened appearance of its abdomen, a word of caution that this elongation does not always obtain seems in order.

It is of interest to note that among the males there are several that have lightly present on their hind tibiae and in a few cases also on their middle tibiae a sticky substance similar to that gathered by workers. The presence of this substance may be a mere accident, but it is noted in passing because the claim has been made that male stingless bees participate in the activities of the hive.

Ducke (1916, p. 77; 1925, p. 387; 1945, pp. 60-61) mentioned a nest observed by Miranda-Ribeiro in the State of Matto Grosso, Brazil, that was located in a hollow tree trunk. The wax of which this nest was constructed was black, the honey abundant and of pleasant taste. As no peculiarities of structure were noted by Miranda-Ribeiro, Ducke inferred that the nest was of the common type, consisting of a brood envelope and combs. At Rockstone, British Guiana, *compressa* was, according to G. E. Bodken, found nesting in the trunk of a tree. According to Miranda-Ribeiro the common name for *compressa* in Matto Grosso is "pé de páu," but Ducke added: "This name is applied to various species that are wont to nest in the lower part of tree-trunks," from which one may perhaps legitimately infer that it is the lower part of the tree that *compressa* favors for the erection of its nest. If so, its habit in this respect recalls that of *fulviventrís* with which *compressa* is structurally rather closely allied.

On the other hand, at La Merced, in the Chanchamayo Valley of Peru, Weyrauch found a nest of *compressa* located in a termite structure plastered against the wall of a house just where a projecting roof gave shelter. Inside the termite structure there was not only the nest of *compressa* but also a rather bewilderingly complex society of *Trigona* (*Trigona*) *chanchamayoënsis*, consisting of five more or less interrelated but rather well-separated brood chambers, with apparently only one physogastric queen present. There were no virgin queens or males in this chain of establishments of *chanchamayoënsis*.

In contrast, the community of *compressa*, laid bare on the same day (March 2, 1940) as that of *chanchamayoënsis*, presented a different picture. Although there was no evidence of royal cells, or even of the queen herself, males were present in abundance. Of 275 specimens from this nest sent me by Weyrauch, all but nine proved to be males.

According to Weyrauch a short cylindrical tube of black wax (1.5 cm. long by 1 cm. in width) gave access to this nest of *compressa*. The nest contained four combs and several jars for the preservation of honey and pollen. These jars were 8 mm. wide and 12 mm. long.

Ducke (1901, pp. 31, 64, under the designation *hyalinata*; 1902a, p. 323; 1902b, p. 315) is authority for the statement that *compressa* visits the blue flowers of *Hyptis mutabilis* and a similar species of Labiatae and also *Protium heptaphyllum*; from *Vismia* species it collects the viscous sap. In Bahia *compressa* was seemingly observed visiting the violet flowers of one of the Compositae that grew there in abundance (Alfken, 1930b, p. 9).

DISTRIBUTION

The species was described from Brazil. Ducke (1925, pp. 387-388) summarized the distribution of *compressa* as follows: "From northern South America to northern Central Brazil and Bolivia an abundant species." His records (1916, p. 77; 1925, p. 388; 1945, p. 60) included Colombia and Surinam on the authority of Friese, Bolivia¹ on the authority of W. A. Schulz, as well as localities in eastern Peru and in the Brazilian States of Pará,

¹ In Friese's type material of *lacteipennis*, a synonym of *compressa*, were likewise specimens from Bolivia.

Amazonas, Acre Territorium, northern Matto Grosso, and Goyaz. Friese's type material of *lacteipennis*, a synonym of *compressa*, included specimens from São Paulo. Alfken (1930b, p. 9) added a locality in the State of Bahia. To the countries listed by Ducke, six (Costa Rica, Panama, Canal Zone, Venezuela, British Guiana, Ecuador) may be added on the basis of the specimens in the present collections, which are from the following localities:

COSTA RICA: San José, Nov., 1911 (W. M. Wheeler).

PANAMA: La Chorrera.

CANAL ZONE: Barro Colorado, June 23, 1924 (N. Banks).

COLOMBIA: Department of Boyacá: Muzo, 900 meters, 1936 (J. Bequaert).

VENEZUELA: Mt. Duida region, Nov. 4, 1928 (G. H. H. Tate).

BRITISH GUIANA: Bartica, May 17, 1901, males; Kartabo, Aug., 1919 (Univ. of Michigan Exped.), Oct., 1920 (Cornell Univ. Exped.), and 1924 (J. F. W. Pearson); Penal Settlement, Bartica District, April 22, 1924 (W. Beebe), Aug. 10, 1920 (W. M. Wheeler); Kamakusa, Jan., 1923, male and workers (H. Lang); Rockstone, Essequibo River, Dec. 27, 1914, "nesting in trunk of tree" (G. E. Bodken), June 26, 1927 (Cornell Univ. Exped.); Matope, June 23, 1924 (J. F. W. Pearson); Waratuk, Feb. 16, 1921, (W. Beebe), May 24, 1929 (J. Ogilvie); Wismar, Nov. 29–Dec. 11, 1934 (A. S. Pinkus); Forest Settlement, Mazaruni River, Aug.–Sept., 1935 (N. A. Weber); Paruiana Mission, Kamarang River, upper Mazaruni District, Oct. 6, 1938 (A. S. Pinkus).

SURINAM: Paramaribo, April 4, 1927 (Cornell Univ. Exped.); Zanderij I., Boven, Para District, April 20, 1927 (Cornell Univ. Exped.).

BRAZIL: State of Amazonas: Esperanza, Aug. 9, 1920 (Cornell Univ. Exped.); Manáos (H. B. Merrill), March, 1945 (W. Praetorius). State of Pará: Pará, March 1901 (A. Ducke); Prata, July 2, 1919 (H. Parish). State of Matto Grosso: Chapada (presumably Sant' Anna do Chapada, near Cuyabá), March–April (H. H. Smith); Cicade Branco, Pôrto Velho, Aug. 20, 1943 (Mark Taylor).

ECUADOR: Sucua, Río Upano, Feb. 3, 1939 (F. M. Brown).

BOLIVIA: Rurrenabaque, Río Beni, Oct. (W. M. Mann); Yungas.

PERU: La Chorrera, Putumayo District, Aug. 17–20, 1920 (Cornell Univ. Exped.); La Sombra to El Encanto, Putumayo District, Aug. 23, 1920 (Cornell Univ. Exped.); La Merced, Valle de

Chanchamayo, 800 meters, March 2, 1939, males (W. Weyrauch).

TRIGONA SUBGENUS PARATRIGONA SCHWARZ

Trigona (*Paratrigona*) Schwarz, 1938, pp. 487–488.

Paratrigona, Moure, 1944a, p. 71.

TYPE SPECIES: *Melipona prosopiformis* Gribodo.

WORKER

DIAGNOSTIC CHARACTERS: Especially differentiated by the following combination of characters: Chitin of at least the head and thorax with dense, fine, very opaque, almost granular sculpturing (a little suggestive of the striking surface of a matchbox). The facial quadrangle relatively narrow, always distinctly longer than wide. The mandible with four teeth along its apex, although these teeth are sometimes blurred through intervening septa of chitin. A yellowish, cream-colored, or white stripe, even if fragmentary or dull, on at least the inner orbit of the eye or part way along the inner orbit, and usually not only the head but the thorax and even the legs with stripe-like or other maculations. The scutellum usually rather flat, extended backward to over-roof the propodeum either only barely or quite extensively; the posterior rim of the scutellum frequently nicked very slightly at the middle. The hairs in most species very sparse, usually silvery gray (rarely partly black); erect hairs, in the rare instances where they are present on the outer face of the middle tibiae, simple as are those along the posterior, as well as the anterior lateral contours of the hind tibiae, those along the anterior lateral contour usually slightly the longer. The hind tibiae triangular to clavate in outline.

HEAD: A little wider than long in some forms (*impunctata* and *isopterothila*), in others subequal and approximately circular in outline. The facial quadrangle narrow, the distance between the eyes at a level just below the anterior ocellus always distinctly less than the distance from the middle ocellus to the apex of the clypeus. The eyes variable from rather strongly convergent to scarcely convergent below. The clypeus usually more than one-half as long as its greatest width, its apico-lateral angles ranging from the some-

what acute (*impunctata* and *isoptrophila*) to the subrectangular; its apex widely truncate along the middle, somewhat less extensively receding to each side. The face of the clypeus is at least somewhat arched. The mandibles overlapping, widest at the base and apex, slightly narrowed towards the middle, the apical edge quadridentate (the second tooth from the outer edge nearly as acute as the other teeth in *impunctata* and *isoptrophila* but rather wide and subtruncate in most forms, the first and second teeth frequently connected by an intervening septum of chitin). Malar space of very uneven development, large towards the outer angle of the base of the mandible but much abbreviated towards the inner angle of the base of the mandible and of different length dependent on the species. The labrum simple. The supraclypeus about as prominent as the clypeus, more or less triangular in contour, longer than wide, its summit connected with the anterior ocellus by a shallow fossa. The middle ocellus barely anterior to the lateral ocelli, somewhat depressed when compared to the lateral ocelli, which appear more prominent because they are somewhat raised and tilted each towards the nearest compound eye; the transverse axis of the middle ocellus usually a little longer than the longitudinal axis. The distance between the lateral ocelli greater than that which separates each lateral ocellus from the nearest compound eye. The region behind the ocelli and about coextensive with them slightly raised or thickened. The chitin densely and finely granular and opaque, black or rarely fulvous, but always with at least some yellow to cream-colored maculations and in the majority of forms with much and varied ornamentation. All of the forms have erect hairs on the lower part of the genal area, on the inferior margin of the mandibles, and on the labrum, but most of them (*impunctata* and *isoptrophila* are an exception) lack or all but lack erect hairs on the front, clypeus, sides of face, and usually the vertex, having only a sericeous sheen over these areas. The scape is about one-half as long as the flagellum and very variable in thickness, in some forms (*lineata* and *opaca*) rod-like and narrower than the flagellum, in others (*prosopiformis* and *haeckeli*) notably swollen, with intermediate

thicknesses characterizing some of the other species.

THORAX: Very densely and finely granular and opaque like the head, only the propodeum with rather coarser and larger sculpturing. The mesonotum measured along the base, where it is widest, a little wider than it is long, but the combined length of the mesonotum and scutellum very notably longer than the mesonotum is wide at the base. The scutellum rather flat and usually large, its length from one-half to three-fifths its maximum width, and extending backward to over-roof the propodeum either only very slightly (*lineata* and *petropolis*) or almost wholly; a very faint nick or feeble indentation often traceable at the middle of the posterior margin of the scutellum. Black with yellowish or cream-colored maculations. Rarely only the posterior half of the pronotum with a transverse stripe, medianly interrupted (in some specimens of *isoptrophila* even this stripe is missing); usually a narrow supplementary transverse stripe likewise over the anterior half of the pronotum (*lineata*, *petropolis*, *prosopiformis*, and *impunctata*). Usually a rather full maculation on the tubercles. Almost invariably (*isoptrophila* is an exception) there is a narrow band bordering the sides of the mesonotum more or less continuously and extending thence either brokenly or entire over the axillae (in *anduzei* the maculation on the axillae may even be wholly lacking) and around the posterior margin of the scutellum, where, however, it sometimes shrinks to a posterior stripe of brief length. Erect hairs almost wholly lacking (except for a few short hairs on the under side of the scutellum and the much longer hairs on the mesosternum) in most *Paratri-gona* workers, although forms so characterized tend to have a sericeous sheen (especially over the mesopleura) that is due to appressed, very microscopic, silvery gray hairs; other forms (*impunctata*, *isoptrophila*, and to a limited extent *lineata*) have erect hairs over some areas where such hairs are lacking in the majority of the forms.

LEGS: Progressively longer from the fore pair to the hind pair, the hind pair approximating or even exceeding in length the entire body (depending upon the degree to which the abdomen is telescoped). The tibiae

of the fore legs shorter than their femora: those of the middle legs about the same length as their femora; those of the hind legs about the same length as their femora plus their trochanters. The contour of the hind tibiae triangular to clavate: their anterior lateral contour almost straight except at the apex where it is rounded; their posterior lateral contour convex; their apex with an inconspicuous angle anteriorly that bears the comb, followed by a curvilinear bulge in the contour that is in turn succeeded by a fairly distinct angulation posteriorly; their outer face gently arched over the basal two-thirds but concave posteriorly over the apical one-third. The inner face of the hind tibiae unevenly gabled, the backward sloping and longer plane without a posterior rim. The hind metatarsi at their widest a little more than one-half the width of their tibiae, their posterior contour convex and rather sharply contracted at the base, the posterior angle of the apex acute and usually somewhat down-directed. The legs more daintly tessellated than at least the head and thorax. The anterior face of the fore and middle femora tends either to be smooth and polished (*impunctata* and *isopterothila*) or to approximate a smooth condition. In all forms the fore and middle tibiae have their outer face tessellated; in *impunctata* and *isopterothila* the hind tibiae are smooth and shiny on their outer face almost from the base to the apex, but in the other known *Paratrigena* the outer face of the hind tibiae is largely tessellated, with only the excavated apical one-third or more smooth or nearly so. The outer face of the metatarsi is tessellated, lightly and sparsely in *impunctata* and *isopterothila*. The hairs abundant only on *impunctata* and *isopterothila*, moderately abundant in *lineata*, rather sparse in the other forms. Erect hairs occur on the hind coxae anteriorly and on the trochanters beneath (although sometimes stunted); no erect hairs on the femora of several species, and sparse and inconspicuous in others; usually at least a few erect hairs on the under side of the fore and especially the middle tibiae, but the external face of these tibiae is devoid of erect hairs except in *impunctata* and *isopterothila*; the hairs fringing the anterior lateral contour of the hind tibiae tend to be longer than those along the

posterior lateral contour, in both cases the hairs are simple and are often short and sparse; a few longer hairs on the outer face of the hind tibiae; the inner face of the hind tibiae densely covered with silvery gray microscopic hairs, with a contiguous patch of such hairs extending upward from the apex of the inner face of the hind femora. The outer face of the metatarsi with few or no hairs in several forms (present in *impunctata*, *isopterothila*, and *lineata*); a more or less developed fringe of hairs along the posterior lateral margin of the metatarsi of especially the fore and middle pair of legs; the usual brushes on the inner face of the metatarsi.

WINGS: With the first discoidal cell about four-fifths to five-sixths the length of the marginal cell. The transverse cubital veins (and more especially the first transverse cubital vein or its upper half) rather strongly to very strongly chitinized in several of the forms, particularly in *opaca* and its varieties, but feeble in others, especially *lineata*. The marginal cell closed or approximately closed. The number of hamuli per lower wing is usually five, rarely four or six.

ABDOMEN: Comparable in width with the thorax. In most *Paratrigena* the chitin of tergite 1 (except the basin-like depression at the base) is granular, and the same type of sculpturing obtains on the exposed apical part of the subsequent tergites (the usually concealed basal part of each tergite when revealed proves, however, to be polished); as a result the abdomen in dorsal view and when telescoped is apt to present a uniformly dull and lusterless surface with sculpturing only barely less dense than that of the head and thorax. The forms *impunctata* and *isopterothila* are exceptional among *Paratrigena* in having tergite 1 largely or wholly devoid of sculpturing and polished and the exposed apical part of tergites 2 to 6 with only very light tessellation (the ordinarily concealed basal part of these tergites polished). The tergites of most forms devoid or virtually devoid of longer hairs but usually with a sericeous sheen over most of their tessellated areas due to the presence of very microscopic appressed hairs. Again *impunctata* and *isopterothila* are exceptional in having semi-erect hairs on the lightly tessellated apical areas of tergites 2 to 6 in

addition to microscopic appressed hairs in these areas. Sternites 1 and 2 with long to moderately long silvery gray erect hairs down their middle, the subsequent sternites with much shorter erect hairs at the middle region of their apex, these hairs sometimes grading into, and in such cases not easy to differentiate from, the silvery gray patches of sericeous hairs at each side of the middle of the apical half of each sternite.

MEASUREMENTS: Length 3.5 to 6 mm.; width of thorax 1.25 to 2 mm.; length of forewing, including tegula, 3.75 to 4.75 mm.

QUEEN

This caste is known so inadequately that it is necessary to omit a general description. (See description of queen of *opaca* variety *pacifica*, p. 384.)

MALE

DIAGNOSTIC CHARACTERS: Especially differentiated by the following combination of characters: Chitin of at least the head and thorax with dense, fine, very dull, almost granular sculpturing (a little suggestive of the striking surface of a matchbox). The facial quadrangle very narrow, the distance from one eye to the other at their level of closest approximation (below) from a little less than one-half to about one-half the distance separating the anterior ocellus from the apex of the clypeus. A yellowish or cream-colored stripe on at least the inner orbit of the eye and usually not only the head but the thorax and even the legs with stripe-like or other maculations. The scutellum usually rather flat, extended backward to over-roof the propodeum either only barely or quite extensively; the posterior rim of the scutellum frequently nicked very slightly at the middle. The hairs even sparser than in the cospecific worker, erect hairs absent or all but absent on the outer face of the fore and middle tibiae of even those species that in the worker have erect hairs in this area, and the hind tibiae with only the most minute of hairs along their anterior lateral margin towards the apex, such hairs being only rarely present (*impunctata*, *isopterophila*) on the posterior lateral margin.

HEAD: Somewhat wider than long. The facial quadrangle much narrower even than

in the worker. The distance between the compound eyes at the level just below the anterior ocellus from five-sevenths (*impunctata*, *isopterophila*) to only a little more than one-half (*prosopiformis*) the distance from the anterior ocellus to the apex of the clypeus. The eyes wider in frontal view than those of the cospecific worker and more emphatically convergent below. The clypeus small, relatively narrower than in the worker, the length being at least two-thirds its greatest width; the sides oblique and divergent from or almost from the base; the apico-lateral extremities rectangular or approximating the rectangular and grazing or virtually grazing the inner orbit of the eyes; the apex widely truncate along the middle and rather sharply receding on each side. The face of the clypeus somewhat arched. The mandibles short; when retracted they have their tips contacting or almost contacting but not overlapping; in outline they are rather thumb shaped, wide at the base, narrowed towards the apex, which is edentate and has the inferior margin convex. The malar space notably shorter than in the cospecific worker, usually surviving only as a tiny triangle near the outer angle of the base of the mandible, the inner angle of the base of the mandible being in contact or approximately in contact with the rim of the eye. The labrum simple. The supraclypeus about as prominent as the clypeus, longer than wide, somewhat triangular in outline, its summit connected with the anterior ocellus by a shallow fossa that is deeper at its start (below) than at its terminus (above). The middle ocellus somewhat anterior to the lateral ocelli, slightly depressed, usually relatively small, frequently with its transverse axis greater than its longitudinal. The lateral ocelli raised and tilted each towards the nearest compound eye. The distance between the lateral ocelli always emphatically greater than that between a lateral ocellus and the nearest compound eye—twice as great or more than twice as great. The region behind the ocelli and coextensive with them as a group slightly raised or thickened. The chitin densely and finely granular and dull, black in the forms from which the male is known (the unknown male of *haeckeli* is presumably bright fulvous like the worker of *haeckeli*),

but always with at least some yellow or cream-colored maculations and in the majority of forms with much and varied ornamentation, frequently exceeding even that of the conspecific worker. All of the forms have erect hairs on the lower part of the genal area, on the inferior margin of the mandibles, and usually on the labrum, but most of them (*impunctata* and *isoptero-phila* are exceptions) lack or all but lack erect hairs on the front, clypeus, sides of face, and usually the vertex. The flagellum from fully three and one-half to nearly four times as long as the scape; the scape variable in width from nearly that of the flagellum to emphatically wider than the flagellum.

THORAX: Finely and very densely granular and dull like the head, only the propodeum with rather coarser and larger sculpturing. The mesonotum measured at the base of somewhat greater width than it is long, but the combined length of the mesonotum and scutellum always very distinctly longer than the maximum width of the mesonotum and likewise somewhat longer than the corresponding measurement in the conspecific worker. The scutellum rather flat and usually large, its length from one-half to fully three-fifths its maximum width, and extending backward to over-roof the propodeum either only very slightly (*lineata* and *petropolis*) or almost wholly; a very faint nick or feeble indentation sometimes traceable at the middle of the posterior margin of the scutellum. There is usually a transverse stripe, often medianly interrupted, along the posterior half of the pronotum but, at least in the limited number of males before me, without any supplementary narrow transverse stripe along the anterior half of the pronotum such as is usual in the conspecific workers of most *Paratrigena* (*lineata*, *petropolis*, *prosopiformis*, and *impunctata*). The tubercles regularly maculated in most forms. Almost always (*isoptero-phila* is an exception) there is a narrow yellowish or cream-colored band that, either entire or fragmented more or less, extends along the lateral margins of the mesonotum, over the axillae (sometimes, as in *impunctata*, with a considerable gap between) and thence (again with sometimes a gap between or continuously) around the posterior margin of the scutellum. Erect hairs

almost wholly lacking (except for a few short hairs on the under side of the scutellum and the much longer hairs on the mesosternum) in *opaca* and *prosopiformis*. Erect hairs, in addition, present dorsally or posteriorly or both on the scutellum of *lineata*, *petropolis*, *impunctata*, and *isoptero-phila*. Some *lineata* males (from Lassance, Brazil) have abundant erect hairs on the mesopleura (and even on the mesonotum) agreeing with their workers, but usually this species and even such relatively hairy forms as *impunctata* and *isoptero-phila* have only stunted or no erect hairs in these regions.

LEGS: Progressively longer from fore pair to hind pair. The tibiae of the fore legs distinctly shorter than their femora, those of the middle legs about as long as their femora; those of the hind legs about as long as their femora plus their trochanters. The hind tibiae somewhat clavate in outline and narrower than in the worker, their anterior lateral contour for the most part rather straight but receding towards the apex, their posterior lateral contour somewhat convex, their apex strongly rounded anteriorly and bluntly rounded to slightly squarish posteriorly, their outer face rather uniformly and gently arched, not or only very slightly flattened or dimpled at the apex and, like the face of the fore and middle tibiae, with at least light tessellation from base to apex. The inner face of the hind tibiae unevenly gabled, the backward sloping and longer plane without a posterior rim. The hind metatarsi elongate (about one-half as long as the associated tibiae) and about half as wide as these, rather parallel sided, the posterior lateral contour virtually straight as is the anterior and without or with only a slight angulation at the apex posteriorly; their outer face, as is that of the outer face of the middle metatarsi, at least lightly tessellated. The small tarsal joints of the hind leg rather elongate, in their aggregate, ranging from about as long (*impunctata* and *isoptero-phila*) to a trifle longer than the hind metatarsi. The legs either maculated or without maculations (*impunctata* and *isoptero-phila*); when maculations are present, they are usually confined to the outer face of the tibiae, sometimes with the addition of the fore metatarsi. The erect hairs usually even

fewer and more stunted than in the case of the conspecific worker. There are erect hairs usually present on at least the hind coxae, on the under side of the trochanters although often much reduced in size or merely tomentose. There is a microscopic fringe sometimes traceable on the under side of the femora, and there are a few erect hairs on the under side of the middle tibiae and sometimes of the fore tibiae towards the apex. The outer face of at least the fore and middle tibiae without erect hairs but with a sericeous sheen, which is present also over the metatarsi and to some extent over the femora. The anterior lateral contour of the hind tibiae with a few inconspicuous stubble-like hairs, sometimes replaced by longer hairs towards the apex, but hairs absent in most forms from the posterior lateral contour of these tibiae. The inner face of the hind tibiae covered densely with minute, silvery gray, microscopic hairs. The metatarsi with fine brushes on their inner face but with few or no hairs on their external face; especially is this true in the case of the middle and hind metatarsi.

WINGS: With the first discoidal cell about four-fifths the length of the marginal cell. The transverse cubital veins (and more especially the first transverse cubital vein or its upper half) rather strongly chitinized to very strongly chitinized in several of the forms, particularly in *opaca* and its varieties, but feeble in others, especially *lineata*. The marginal cell closed or approximately closed. The number of hamuli per lower wing usually five, rarely four or six.

ABDOMEN: Comparable in width with the thorax. In most *Paratrígona* the chitin of tergite 1 (except the basin-like depression at the base) is granular, and the same type of sculpturing characterizes the exposed apical part of the subsequent tergites (the usually concealed basal part of each tergite varies from an almost polished surface to one in which the sculpturing approximates the density of the exposed part). As a result the abdomen in dorsal view and when telescoped is apt to present a uniformly dull and lusterless surface with sculpturing only barely less dense than that of the head and thorax. The forms *impunctata* and *isoptero-phila* are exceptional among *Paratrígona* in having tergite 1 largely or wholly devoid of sculpturing and

polished and the basal area, at least, of tergite 2 also polished (*impunctata*) or at the most with only very fine sculpturing (*isoptero-phila*), while the apical part of this tergite is finely tessellated. The subsequent tergites also with their apex tessellated; the usually concealed basal part of each of these tergites either virtually smooth (*impunctata*) or tessellated very lightly (*isoptero-phila*). The dorsal aspect of the abdomen of most *Paratrígona* without erect hairs but, when the tergites are telescoped, with a feeble sericeous sheen due to microscopic appressed hairs that are absent from the usually concealed basal part of the tergites. The forms *impunctata* and *isoptero-phila* with hairs over the apex of tergites 2 to 6 that are less developed than those in the corresponding area of the worker. Tergite 7 fringed apically with rather long hairs. The sternites silvery gray sericeous to silvery gray tomentose. Sternites 4 and 5 usually of rather distinctive structure, one or both deeply emarginate at the middle of the apex and sometimes with tubercles or other distinctive armature. Sternite 6 with its median element elongate spine-like only in *lineata* and *petropolis*, usually with a short triangular spine or even lobe-like (*opaca*).

MEASUREMENTS: Length 3.75 to 6 mm.; width of thorax about 1.5 to 2 mm.; length of forewing, including tegula, 4 to 5 mm.

DISCUSSION

The subgenus *Paratrígona*, which Moure (1944a, p. 71) has recently raised to generic rank, is interesting both from the standpoint of its structure and its habits. Alone among the Meliponidae, it shares with the subgenus *Trígona* a mandible that is completely toothed from end to end. But even this resemblance is somewhat deceptive, for the number of teeth is four in *Paratrígona* and usually five, only exceptionally four (*fulviventris* and *compressa* and possibly *braueri*), in *Trígona*, while the teeth themselves do not closely correspond in shape between the one subgenus and the other. In nearly all other respects *Paratrígona* is remote from *Trígona*, having densely sculptured chitin which in *Trígona* is smooth, and having only simple hairs (and those usually very short) fringing the hind tibiae of the worker where *Trígona*

has usually an abundance of feathered hairs. The granular to tessellated character of the sculpturing of *Paratrigona* is shared or approximated by members of the New World subgenera *Schwarziana*, *Parapartamona*, and *Cephalotrigona*, by certain of the *Hypotrigona* and by certain *Scaptotrigona*. In accord with members of the subgenus *Nannotrigona*, species of *Paratrigona* tend to have a backward extended scutellum, which, however, lacks the deep posterior emargination of *testaceicornis* and its relatives. As in some or all of the species of a number of the subgenera of *Trigona* (notably *Tetragona*, *Plebeia*, *Partamona*, *Schwarziana*, *Parapartamona*, *Nannotrigona*, and *Cephalotrigona*) as well as in many *Melipona*, the present subgenus is often extensively maculated, and some of its forms attain a richness of ornamentation that tends to make them preëminent in appearance among the stingless bees. The rather elongate facial quadrangle of some of the forms of *Paratrigona* (most strikingly evidenced by the males) adds to their rather distinctive appearance, and the males furthermore often possess a diversity of armature on some of the abdominal sternites (particularly sternites 4 to 6) that make them structurally very interesting.

A structural peculiarity of some *Paratrigona* (notably *prosopiformis* and *haeckeli*) is the swollen scape. The diameter of the scape varies indeed considerably within *Paratrigona* and, because it seems a character in which specific independence is asserting itself in this group, I have given specific rank to forms that showed such a tendency to separate themselves from species with which they were otherwise wholly or in the main identical. This applies particularly to *petropolis* and *isopterophila*, respectively very close to *lineata* and to *impunctata*. Where structural differences are very slight, I have been inclined in other instances to accord only varietal rank to such departures from the standard structure. Cases in point are *opaca* variety *guatemalensis*, *opaca* variety *anduzei*, and *opaca* variety *ornaticeps*, which, notwithstanding the fact that they have a slightly longer malar space than typical *opaca*, seem to me on the whole too close to that species to be accorded independent specific rank. Throughout the Meliponidae

instances occur where it is very hard to make an arbitrary decision as to whether specific or varietal recognition best expresses the status of the bee described, and my own hesitation is indicated by the fact that originally I described *isopterophila* as merely a subspecies of *impunctata*.

One supplementary respect in which at least the only available example of the male of *isopterophila* seems to differ from the few examples of the corresponding sex of *impunctata* before me is in the slightly less feeble tessellation on the usually concealed basal part of the successive abdominal tergites. This character has almost the status of a sexual distinction in the subgenus, for in the worker this basal area is usually polished while in the conspecific male it is sometimes sculptured, at least lightly. Possibly its absence in the worker is correlated with wax production. It has been stated that the male in the Meliponidae, like the worker, is capable of producing wax, a contention that, it seems to me, is possibly still open to question. In *Paratrigona*, at least, the difference in the sculpturing of the two castes in the areas where in the worker the wax is produced strengthens the doubt whether wax-production is a function of the male.

The nesting sites selected by this subgenus are among the most interesting recorded, especially in view of the frequency with which *Paratrigona* ensconces itself in the nests of other social insects. Some species (*impunctata* and *isopterophila*) favor the nests of termites (a habit shared, however, by certain species of other subgenera), while at least typical *opaca* and *lineata* variety *nuda* are known to erect their colonies in the nests of ants, the former having been collected by J. Bequaert in a nest of *Dolichoderus bispinosus* (see p. 377) and the latter repeatedly by W. Weyrauch in the deserted subterranean compartments of *Atta sexdens* (see p. 366; pl. 7).

The presence of a stingless bee colony in a nest of *Camponotus senex* variety *textor* was reported by Forel (1904, p. 47; 1905, pp. 170-171; 1928, vol. 1, p. 357; vol. 2, p. 282). The Neotropical *Camponotus senex*, like *Cecophylla smaragdina* of the Old World, constructs one of the most interesting of ants' nests, a structure built of the silk

emitted by the larvae, which are used by the adult ants as shuttles in weaving the nest fabric. Unfortunately the species of bee that had a nest established in the heart of this structure of silk is not mentioned by Forel. It would seem likely that it was a member of *Paratrigona*, but the conclusion is far from absolute.

Association of stingless bee with ant in a composite nest is not peculiar to *Paratrigona*. H. von Ihering (1903, p. 218) recorded finding a nest of *Trigona* (*Trigona*) *fulviventr*is variety *guianae* Cockerell which likewise was located in the interior of an ants' nest, while Marianno (1911, p. 81) expressed the opinion that *Trigona* (*Schwarziana*) *quadripunctata* variety *bipartita* used the deserted formicaries of *Atta sexdens* for the establishment of its nests. Thus the myrmecophilous tendency is sometimes manifested by species other than those belonging to *Paratrigona*. The ants' nest in which was established the colony of *Trigona* (*Trigona*) *fulviventr*is variety *guianae* "filled entirely," according to von Ihering's statement, "a very spacious hollow, nearly one meter in diameter, in the base of a thick trunk and in part in the roots. The bee nest was surrounded on all sides by the nest mass of the ants."

Trigona (*Paratrigona*) *lineata* variety *nuda* was not the only *Trigona* observed by Weyrauch that availed itself of the conveniences offered by the nest of the ant *Atta sexdens*. In addition, he noted colonies of what proved to be a member of the subgenus *Partamona* in an abode of these ants, and the same observer found that members of this subgenus, including two instances of *Trigona* (*Partamona*) *testacea* variety *testacea* Klug, had established their nests, No. 136 and No. 137, in nests of *Atta cephalotes* at Satipo, Peru.

Although a nest of *amalihea* mentioned by A. Emerson was erected not in an ants' nest but in that of a termite, it is of interest to note that "ants of the species *Anochetus* (*Stenomyrmex*) *emarginatus* Fabricius (det. W. M. Wheeler) were also found in abundance occupying deserted cells of this termite nest" (Schwarz, 1938, p. 457). Tarlton Rayment (1935, p. 526) quoted a Mr. Lang to the effect that a Rhodesian *Trigona* with the native name of "M'bongolwane," "makes its nest in 'mopani' ground, usually an ants'

nest," but whether the term "ant" is here used in the myrmicine sense or as synonymous with termite (the so-called "white ants") is not clear.

While the recorded instances of the establishment of *Trigona* colonies within the nests of ants are relatively few, it is astonishing in a way that this habit should have been formed and that it has persisted, for ants are commonly considered among the worst enemies of stingless bees. Of course, the association is robbed of its peril when the site selected is the deserted, as opposed to a populous, nest of an ant. Nevertheless the selection by the bee of a nest site in the very citadel of the enemy is akin to the bravado of the water ouzel in building its nest almost in contact with the descending cataract.

Hardly less interesting than the selection of an ants' nest as the site for a colony are the instances, no fewer than three in number, where a member of the subgenus *Paratrigona*, namely, *opaca* variety *pacifica*, founded its colony in the nest of a bird. This unusual place of abode has been recorded in the case of certain bumblebee species and also by Salt (1929, p. 437) for the stingless bee *Melipona favosa* variety *favosa*, but it is thanks to the vigilance of Weyrauch that we have come to appreciate how ornithophilous a given form may be. A nest which *pacifica* founded in the root tangle of orchids was also noted by him.

Subterranean nests of *Paratrigona* were reported (H. von Ihering, 1903, p. 205) in the case of another species (alluded to as *bilineata* Say but probably *petropolis*), while Marianno (1911, pp. 81-82) listed nests built in trees and in the crevices of walls, interpreting them incorrectly, I think, as those of *bilineata* Say.

The brood cells of *Paratrigona* are, so far as known, arranged compactly in horizontally placed combs, not in clusters as are those of the subgenus *Hypotrigona*, which has a somewhat superficial likeness to *Paratrigona* because of resemblances in the sculpture of the chitin.

KEYS TO THE SPECIES AND VARIETIES OF *Trigona* (*Paratrigona*)

WORKERS

1. The head, thorax, and abdomen ferruginous, with pale maculations on the head and

- thorax. The scape considerably wider than the flagellum *haeckeli* Friese
- The head and thorax and usually also the abdomen black; at least a stripe along the inner orbit or part way along the inner orbit of the eyes (although sometimes dull) and usually both face and thorax conspicuously maculated with yellow or cream color or white 2
2. Tergites 1 and 2 of the abdomen extensively polished, with merely very feeble tessellation (largely absent from tergite 1) along their apical one-third. The apex (usually the only part visible) of the subsequent tergites with slightly stronger tessellation, but very feeble nevertheless compared to the dense, rather granular tessellation on head and thorax. The tessellated areas on the tergites (especially in the case of tergites 3 to 6, to a lesser extent in the case of tergite 2) co-extensive with a hirsute band of appressed to semi-erect, brownish to grayish hairs. 3 Tergite 1 (except in the largely sculptureless, basin-like depression at the base of tergite 1) and the exposed part of tergite 2 uniformly and densely tessellated, as dull or nearly as dull in most instances as the head and thorax. The subsequent tergites with strong sculpturing along their apices, so that, when telescoped, the dorsal aspect of the abdomen presents usually a lusterless, uninterrupted surface of almost granular appearance. The tergites without bands of hair 4
3. The scape no wider than the flagellum. The clypeus with a stripe (sometimes medianly obliterated) along its apex. The mesonotum more or less banded on each side. *impunctata* Duche
- The scape at its widest a little wider than the flagellum. The clypeus without an apical stripe. No bordering stripe along each side of the mesonotum. *isopterothila* Schwarz
4. The scape greatly thickened, considerably wider than the flagellum and swollen in appearance. The thorax elongated, the scutellum extended backward so far that, when the insect is viewed from above, the scutellum conceals much of the propodeum. Rather robust, up to 6 mm. in length. *prosopiformis* Gribodo
- Not having the combination of characters indicated. Smaller, usually not more than 4 mm. in length 5
5. The antennae moderately long: the scape when in vertical position extending somewhat more than one-half the way to the anterior ocellus; the intermediate joints of the flagellum as long as, or a little longer than, they are wide. The scutellum relatively short, about twice as wide as it is long, not strongly over-roofing the propodeum. The tubercles deflected somewhat from the horizontal to the vertical. The supraclypeal maculation trapezium shaped to almost triangular 6
- The antennae distinctly short: the scape when in vertical position extending only about halfway to the anterior ocellus; the intermediate joints of the flagellum wider than long. The scutellum about three-fifths as long as it is wide, of considerable backward extension so that, when viewed from above, it conceals much of the propodeum. The tubercles vertical or almost vertical. The supraclypeal maculation of up-pointed arrow shape (sometimes the arrow is vestigial or broken or even absent) or a solid triangle of yellow or barely trapezium shaped. 8
6. The scape slightly thickened, comparable in width to the flagellum and at its middle wider than the flagellum, black or predominantly black, sometimes partly dark reddish in front, especially towards the base. The maculations on the clypeus almost always reduced to a median longitudinal stripe and two isolated spots, one in each of the anterolateral angles. The mandibles usually reddish apically, black basally; the labrum reddish or blackish *petropolis*, new species
- The scape rod-like, narrow, with a well-defined pale to yellowish stripe. The clypeal maculation almost always entire, the transverse stripe of irregular thickness and contour that extends along the apical margin of the clypeus being in contact with the perpendicular median stripe, forming a united figure. The mandibles and labrum usually yellowish, sometimes slightly invaded by reddish. 7
7. A usually rather massive stripe down the middle of the clypeus, forming the shaft of a somewhat anchor-shaped figure, the arms of which follow the angulations of the apex of the clypeus. The scutellum with silvery gray, erect to semi-erect hairs that are especially abundant near or along the posterior margin, where they tend to grow more or less horizontally; the mesopleura also usually with erect, silvery gray hairs. *lineata* variety *lineata* Lepeletier
- The median perpendicular stripe on the clypeus relatively short and slender, shaped somewhat like a fool's cap and up-pointing, its upper extremity separated by an area of black from the supraclypeal maculation.

- The scutellum and mesopleura devoid of erect hairs. *lineata* variety *nuda* Schwarz
8. The maculations of the clypeus confined to the apical one-half of the clypeus. The supraclypeal maculation, if present, consists either of an up-pointing angle (like an arrowhead) bounding a dark triangular area or of the fragmentary remains of such an up-pointing angle, usually represented by two upwardly converging brief lines (frequently more or less obliterated) that fail to unite. The mesopleura and metapleura immaculate. 9
- The maculation of the clypeus not confined to the apical one-half of the clypeus. The supraclypeal maculation a solid triangle of yellow or barely trapezium shaped. 12
9. The malar space relatively short, at its shortest (near the inner angle of the mandible) barely one-half as long as the flagellum is wide. The maculations stronger and more extensive. An irregular transverse stripe (expanded usually at each end) along the apex of the clypeus. The stripe along the sides of the mesonotum and axillae confluent with the stripe that rims the scutellum posteriorly. The stripe on the outer face of the fore and middle tibiae extending from the base to well beyond the middle of the joint. 10
- The malar space relatively long, at its shortest (near the inner angle of the mandible) about as long as the flagellum is wide. The maculations either limited in extent or more or less subdued. The yellow transverse stripe on the clypeus either semi-extinguished, especially along the middle, abbreviated, or absent. The stripe along the side of the mesonotum (and frequently over, or part way over, the axillae as well) separated more or less from the stripe that rims the posterior margin of the scutellum. The maculation on the outer face of the fore and middle tibiae confined to the base. 11
10. The maculations light yellow
 *opaca* variety *opaca* Cockerell
 The maculations pure white
 *opaca* variety *lundelli* Schwarz
11. The scape with a well-developed stripe in front. The axillae with a stripe that is wider (at least at the apex) than the lateral stripe of the mesonotum and that extends the full length of the axillae. The maculation on the outer face of the hind tibiae confined to the base. *opaca* variety *guatemalensis* Schwarz
- The scape wholly coal black. The axillae either immaculate or with a fragmentary or speck-like maculation. The hind tibiae with a

- stripe along the posterior margin of the outer face from the base almost to the apex although taperingly
 *opaca* variety *anduzei* Schwarz
12. The head less extensively ornamented. No bordering stripe along the outer (only along the inner) orbit of the eye. No maculation on the front. No maculation on the mesopleura or metapleura
 *opaca* variety *pacifica* Schwarz
- The head more heavily ornamented, with a stripe not merely along the inner orbit of the eye but prolonged along the outer orbit to encircle or nearly encircle the eye. The front more or less extensively maculated. The mesopleura and metapleura with a maculation 13
13. The malar space at its shortest (near the inner angle of the mandible) relatively long, about as long as the flagellum is wide. A yellow band across the vertex. A yellow spot sometimes on each side of the bare middle area of the propodeum
 *opaca* variety *ornaticeps* Schwarz
- The malar space at its shortest little more than linear, its length rather less than one-half the width of the flagellum. No band across the vertex. No maculations on the propodeum
 *opaca* variety *lineatifrons* Schwarz

QUEENS

(Too few of the queens of *Paratrigona* are known to justify a key to the royal caste.)

MALES

(The male of *haeckeli* and of several of the varieties of *opaca* is unknown.)

1. Tergite 1 of the abdomen almost wholly smooth, tergite 2 with its basal two-thirds either polished or, as is apex, with feeble tessellation. Sternite 5 truncate along the apex (except for a narrow subrectangular median emargination) and very wide at the apex, so wide that, when the insect is viewed from above, the sternite is seen jutting out to each side as a strong shoulder-like angle fringed with rather long hairs. The widely triangular median element of sternite 6 distinctly short, not or barely extending beyond the shoulder-like lateral elements of sternite 6 2
- Tergite 1 (except for the basin-like depression at the base) and the exposed part of tergite 2 uniformly and densely granular. Sternite 5 with the lateral elements rather widely sundered by a large median emargination; no part of this sternite visible when the bee is

- viewed from above. The median element of sternite 6 extending well beyond the sides 3
2. The scape slightly wider than the flagellum. A narrow border of yellow rimming more or less continuously the sides of the mesonotum, the axillae, and posterior edge of scutellum *impunctata* Ducke
The scape nearly twice as wide as the flagellum. The mesonotum and scutellum immaculate *isopterophila* Schwarz
3. The scutellum extended backward almost as far as the down-sloping propodeum, so that, when the insect is viewed from above, the propodeum is largely concealed. The tibiae with stripes that extend to or nearly to the apex. The median element of sternite 6 widely to very widely triangular. 4
The scutellum extended backward only very moderately, far from completely over-roofing the propodeum, a large section of which remains visible when the leveled insect is viewed from above. The fore and middle tibiae with merely basal spots. The median element of sternite 6 elongate, narrow, and spine-like 5
4. The scape much thickened, swollen, with a notably greater diameter than that of the flagellum. Sternite 4 with two rather large tubercles along the apex that are separated from each other by a space considerably less than the width of either tubercle. Sternite 5 with each of its widely sundered lateral halves armed at the inner end of their apex by a rather club-shaped, inward and downward extended, somewhat elongate protuberance. Fairly robust for *Paratrigona*, with a forewing length, including the tegula, of about 5 mm. *prosopiformis* Gribodo
The scape barely thicker than the flagellum. Sternite 4 with two small tubercles along the apex that are separated from each other by a space much greater than the width of either tubercle. Sternite 5 with its widely separated and much reduced lateral elements of angular outline along their apex and with a tiny denticle at their inner extremity, but otherwise unarmed. Smaller; length of forewing, including tegula, about 4 mm.
. *opaca* variety *opaca* Cockerell
5. The scape not any thicker than the flagellum. The clypeus usually wholly cream colored except for two short, dark, parallel, longitudinal stripes. The stripe rimming the posterior contour of the scutellum confluent or virtually confluent with a stripe extending along the lateral margin of the mesonotum

to the inclusion of the axillae.

. *lineata* Lepeletier
The scape at its middle of greater diameter than flagellum. The clypeus mostly dark, usually with a maculation only along apical edge, and often even this maculation with a wide median interruption, resulting in two sundered spots, one in each of the anterolateral angles of the clypeus. The stripe posteriorly on the scutellum relatively short, distinctly and widely separated from the stripe that extends along the lateral margin of the mesonotum to the inclusion of the axillae *petropolis*, new species

**Trigona (Paratrigona) lineata variety
lineata (Lepeletier)**

- Melipona (Trigona) lineata* LEPELETIER, 1836, p. 430.
Melipona lineata, LUCAS, 1889, pp. cvii-cviii.
Melipona lineata, DALLA TORRE, 1896, p. 580.
? *Trigona lineata*, FRIESE, 1908b, p. 93.
Trigona lineata, DUCKE, 1910b, p. 368.
Trigona lineata, MARIANNO, 1911, p. 115.
Melipona lineata, DUCKE, 1916, opposite p. 28, pp. 104-105 (in part).
? *Trigona lineata*, COCKERELL, 1917, p. 127.
Trigona bilineata, LUTZ, 1924a, pp. 205, 207, 208, 209, 216, 220, 221, 222.
Melipona lineata, DUCKE, 1925, pp. 343, 352, 400-401 (in part).
Trigona lineata, SCHWARZ, 1932a, pp. 253, 259.
Trigona (Paratrigona) lineata, SCHWARZ, 1938, pp. 493, 494, pl. 59, figs. A, A', B, B'.
Trigona lineata, R. VON IHERING, 1940, pp. 436, 480.
Trigona (Paratrigona) lineata, MOURE, 1943, p. 147.
Melipona lineata, DUCKE 1945, opposite p. 24, pp. 80-81 (in part).

WORKER

DIAGNOSTIC CHARACTERS: Black with maculations. Scape narrow and rod-like, rather slender compared with the flagellum; intermediate joints of flagellum as long as, or a little longer than, wide. Facial maculations cream colored to somewhat yellowish, consisting of a full-length stripe anteriorly on scape, a stripe (narrowing above) along inner orbit of eye to about level of middle ocellus, a small trapezium-shaped spot in supra-clypeal area, a usually somewhat anchor-shaped figure on clypeus with median shaft rather thick. Labrum and mandibles

also maculated. Scutellum about half as long as wide. The maculated tubercles deflected somewhat from the horizontal to the vertical. A narrow, cream-colored stripe along the sides of the mesonotum and continuous around the posterior margin of the scutellum, slightly expanded over the axillae. Erect hairs on scutellum and, usually, mesopleura. Abdomen, when telescoped, uniformly dull above owing to dense tessellation.

HEAD (FIG. 54A): Nearly as long as wide, approximating the circular, not quite so wide as the distance separating the outer rim of one of the tegulae from the outer rim of the other tegula. The face narrow, the distance between the compound eyes at a level just below the middle ocellus only about two-thirds that between the middle ocellus and the apex of the clypeus. The compound eyes somewhat convergent below, the distance that separates them at their level of closest approximation (below) being about as 4 is to 4.5 when compared to their divergence at the level just below the middle ocellus. The clypeus more than one-half as long as it is wide, gently arched, a little more elevated than the sides of the face, six sided, the apex widely truncate along its middle and more briefly but sharply receding to each side, the apicolateral angles approximating the rectangular and narrowly but distinctly separated from the nearest compound eye. The supraclypeus about as prominent as the clypeus. The labrum slightly and rather evenly thickened, not tuberculate. The mandibles (fig. 54A1) overlapping each other, wider at base and apex than at the middle; in perfect specimens with four apical teeth but these sometimes worn down and not always clearly traceable, and the outermost tooth frequently connected by a septum of chitin with the rather wide blunt tooth that adjoins it. The malar space subtriangular, large on its outer half or more but sharply shortened towards its inner extremity. The distance between the lateral ocelli (about twice the major axis of an ocellus) distinctly greater than that which separates each lateral ocellus from the nearest compound eye. The region behind the ocelli barely thickened. The sculpturing of the head, as is that of most of the other parts, exceedingly dense and fine, the entire head

viewed from in front being dull and opaque owing to a microscopic granular surface (a little suggestive of the striking surface of a matchbox) that is utterly devoid of shiny interspaces; the sculpturing somewhat finer on the cheeks, especially the lower third of the cheeks, which in some specimens are faintly shiny. The scape narrow and rod-like, rather slender compared to the flagellum and about one-half its length. The head black with the following cream-colored to slightly yellowish maculations: a stripe from base to apex on the scape in front; a stripe (somewhat wider below than above) extending along the entire inner orbit of the eye almost to the level of the anterior ocellus; a small, rather trapezium-shaped spot in the supra-clypeal area; a usually rather massive stripe down the middle of the clypeus, forming the shaft of a somewhat anchor-shaped figure, the arms of which follow the angulations of the apex of the clypeus. The labrum sometimes invaded by reddish; the mandibles sometimes invaded by reddish and with at least the apex reddish and the basal prominences blackish. The head almost completely devoid of erect hairs, which are confined to the lower one-third of the genal area, the inferior margin of the mandibles, the labrum, and sparsely on the vertex. The hairs on the labrum and mandibles tend to be ochraceous to silvery, those on the lower one-third of the genal area and vertex silvery. In addition to these few erect hairs there is a sericeous sheen due to the presence over most of the head of dense, appressed, very microscopic, silvery gray hairlets. The upper two-thirds of the cheeks silvery gray pruinose.

THORAX: Sculptured like the head, exceedingly densely and finely granular, with resulting opacity; only on the propodeum is the sculpturing a little less delicate and less crowded. The width of the mesonotum at its maximum, near the anterior margin, a little greater than its length (about as 6 is to 5); the combined length of the mesonotum and scutellum compared to the maximum width of the mesonotum about as 7 is to 6. The scutellum about twice as wide as it is long, its posterior rim (in rare cases notched at the middle) slightly over-roofing the basal part of the propodeum, which extends backward

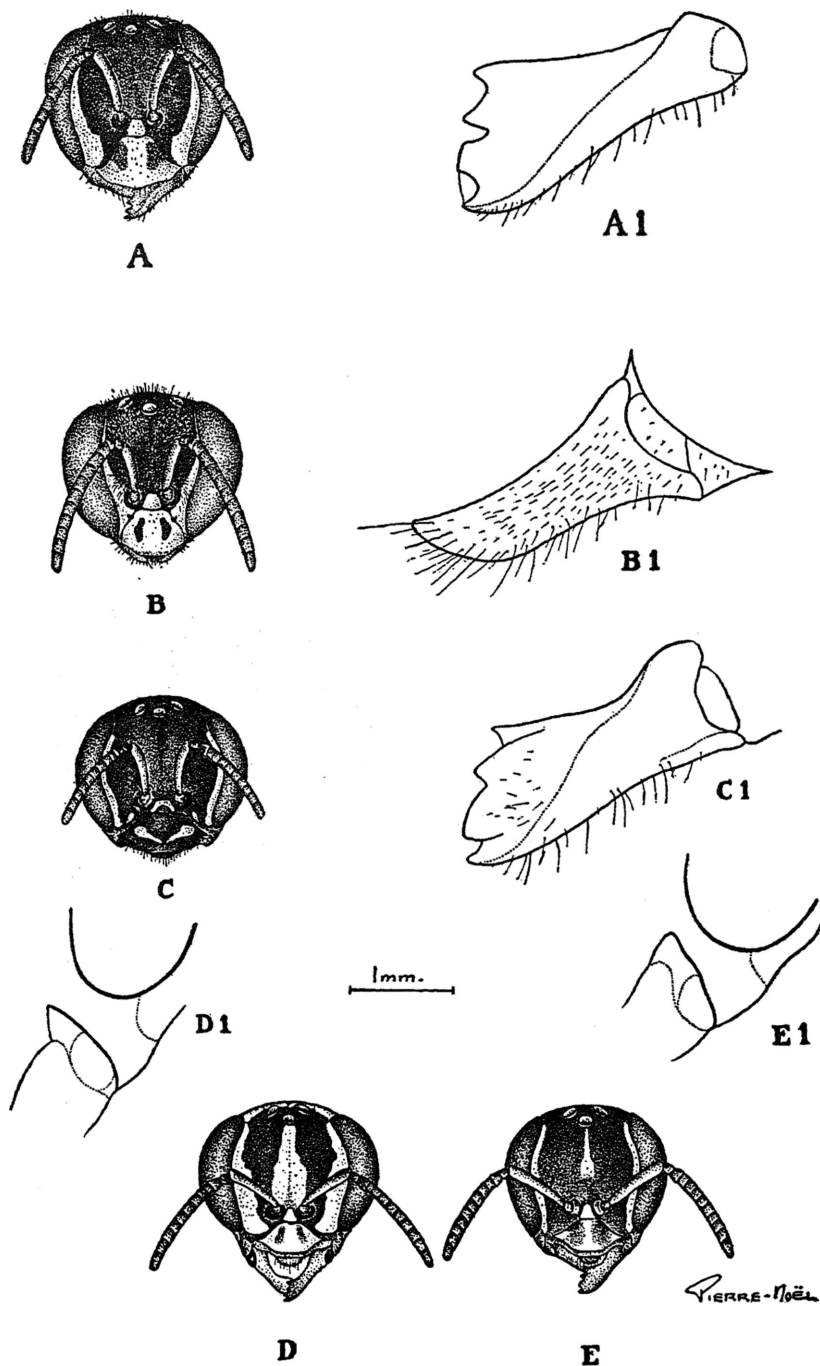


FIG. 54. Head of worker (A) and male (B) of *Trigona* (*Paratrigona*) *lineata* variety *lineata* (Lepeletier), and worker (C) of *Trigona* (*Paratrigona*) *opaca* variety *opaca* Cockerell, with their respective mandibles (A1, B1, C1); worker (D) of *Trigona* (*Paratrigona*) *opaca* variety *ornaticeps* Schwarz, and worker (E) of *Trigona* (*Paratrigona*) *opaca* variety *lineatifrons* Schwarz, with their respective malar space (D1 and E1). Drawings by V. Pierre-Noël.

for a distance approximating the length of the scutellum. The tubercles deflected somewhat from the horizontal to the vertical, a little resembling in shape a mussel shell. The erect hairs are usually absent from the mesonotum and, when they occur (specimens from Lassurance), are sparse and silvery gray. The scutellum with silvery gray, erect to semi-erect hairs that are especially abundant near or along the posterior margin, where they tend to grow more or less horizontally (these hairs are shorter in the specimens from Argentina than in those from Brazil); and the mesopleura also usually with short, erect, silvery gray hairs. The mesonotum, mesopleura, and scutellum usually with a sericeous sheen due to their being covered densely with very microscopic, silvery gray appressed hairlets. The mesosternum with long, fairly dense, silvery gray hairs. The propodeum bare on the large dorsal and middle area but flanked on each side by a dense conspicuous patch of silvery gray to whitish tomentum. The thorax mainly black. The pronotum has a cream-colored transverse stripe (usually interrupted medianly) along its posterior margin, and there is a much narrower transverse band of similar coloration usually along its anterior margin; the tubercles are cream colored. A narrow border of cream color rims continuously the sides of the mesonotum, the axillae, and the posterior edge of the scutellum, being of virtually uniform width except for a slight dilation on the axillae.

LEGS: Sculptured more delicately than the other parts of the body, with usually the hind tibiae smooth and somewhat shiny towards the apex. Reddish brown to brownish black, with a short, cream-colored stripe externally at the base of all the tibiae, longest on the hind tibiae. The legs with a pale sericeous sheen, more especially on the hind femora and the external face of the fore and middle tibiae and the external face of the middle and hind metatarsi, but with erect hairs somewhat few. Such erect hairs are silvery gray and are present on the coxae (particularly the hind pair anteriorly) and on the trochanters (especially the middle pair), sparse on the under side of the fore tibiae, more abundant and longer on the under side of the middle tibiae (the external face of both fore and middle tibiae devoid or virtually devoid of erect hairs), a fringe on the anterior

lateral contour of the hind tibiae (fig. 55A) that, though sparse, consists of rather longer hairs than the fringe along the posterior lateral contour of these tibiae, scattered hairs also on the external face of the hind tibiae, a fringe on the anterior lateral contour and especially on the posterior lateral contour of the fore and middle metatarsi, and a fringe of rather shorter hairs on the lateral contours of the hind metatarsi. The metatarsal brushes tend to be light golden.

WINGS: Uniformly clear and transparent, iridescent. The venation and stigma brownish to fuscous, with the transverse cubital veins only rather feebly demarked. The tegulae bright ferruginous with a distinct cream-colored maculation anteriorly and a similar maculation usually also at the base of the wing. The number of hamuli per hind wing is usually five, rarely six. Of 154 wings counted, 144 had five hamuli and 10 had six hamuli, an average of 5.06.

ABDOMEN: Usually black, more rarely ferruginous (callows?).¹ When telescoped, which is usually the case, the tergites present a uniformly tessellated to granular appearance devoid of shiny interspaces. When the abdomen is extended, however, the usually concealed basal areas of the tergites prove to be polished. The sternites more lightly and less densely sculptured than the tergites. The dorsal aspect of the abdomen devoid or virtually devoid of longer hairs (a few sometimes apico-laterally), but the tergites usually have a sericeous sheen over their sculptured areas due to the presence of very microscopic appressed pale hairs.

MEASUREMENTS: Length 3.5 to 4.5 mm.; width of thorax about 1.5 mm.; length of forewing, including tegula, 4 to 4.5 mm.

QUEEN

"Head very narrow; malar space fairly large. Mesonotum much broader than long; scutellum not projecting and forming with

¹ Among specimens even with identical data and representing large series, considerable range of coloration may be noted in the abdomen, and the specimens of lighter abdomen I should be inclined to regard as callows. Ducke, on the other hand, makes the following observation (1925, p. 400) regarding *lineata*: "The abdomen is black or brown in specimens from the Amazon, but black or red in creatures from central and south Brazil." The specimens from the Amazon are probably what is here designated *opaca* Cockerell.

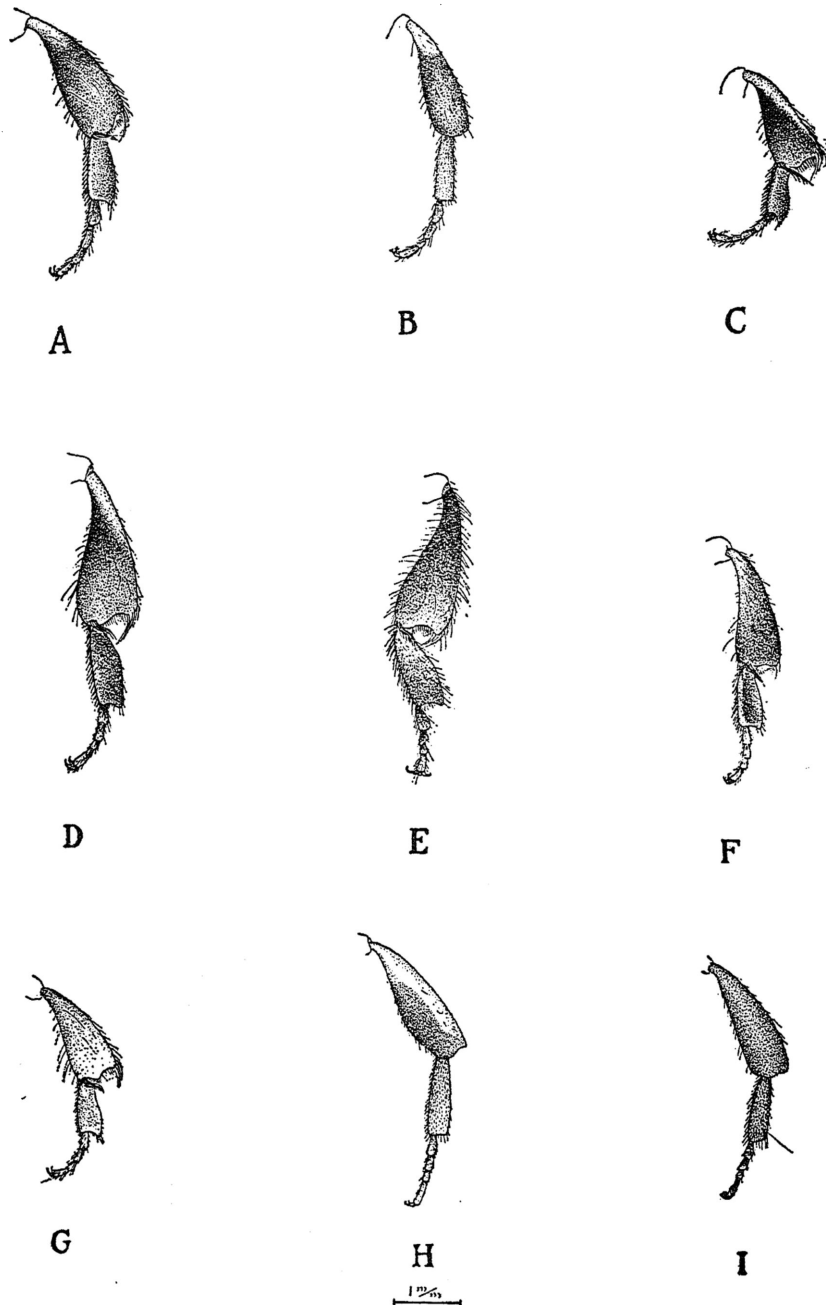


FIG. 55. Hind tibia, metatarsus, and small joints of the tarsus of worker (A) and male (B) of *Trigona* (*Paratrigona*) *lineata* variety *lineata* (Lepeletier); worker (C) of *Trigona* (*Paratrigona*) *opaca* variety *opaca* Cockerell; worker (D) and male (H) of *Trigona* (*Paratrigona*) *prosopiformis* Gribodo; worker (E) of *Trigona* (*Paratrigona*) *isoptrophila* Schwarz; worker (F) of *Trigona* *schrottkyi* Friese; worker (G) of *Trigona* (*Paratrigona*) *haeckeli* Friese; male (I) of *Trigona* (*Paratrigona*) *impunctata* (Ducke). Drawings by V. Pierre-Noël.

the upper part of the propodeum an inclined plane (*eine schiefe Ebene*). Hind tibiae narrow, arched with the exception of a small impression at the apex. Hind metatarsi long, bent in the basal part. Yellow maculations as in the worker" (Ducke, 1916, p. 105; 1925, p. 400; 1945, p. 80).

MALE

HEAD (FIG. 54B): Somewhat wider than long, in the proportion of about 8 to 7, sub-circular in contour, a little narrower than the distance between the outer rim of one of the tegulae and the outer rim of the other. The face very narrow. The distance from one eye to the other at their level of closest approximation (below) is less than one-half the length of the eye, whereas in the worker the shortest distance between the eyes is about two-thirds of the length of the eye. The distance that separates the eyes at their level of closest approximation about as 3 is to 4 when compared with the distance between them at the level just below the anterior ocellus, and about as 3 is to 6.5 when compared to the distance separating the anterior ocellus from the apex of the clypeus. The clypeus fully two-thirds as long as wide, small, rather distinctly arched, six sided, the apex widely truncate along the middle and rather sharply receding on each side, the apico-lateral angles approximating the rectangular and grazing the inner orbit of the eye. The labrum simple. The mandibles (fig. 54B1) somewhat thumb shaped in outline, rather wide at the base, running to a point at the edentate apex, rather short, their tips meeting (not overlapping), the inferior margin convex in outline towards the apex. The malar space surviving only as a tiny triangle near the outer angle of the base of the mandible, the inner angle of the base of the mandible being in contact with the rim of the eye. The distance between the lateral ocelli about twice the major axis of an ocellus; the distance between a lateral ocellus and the nearest compound eye a little less than the diameter of such an ocellus. The region behind the ocelli barely thickened. The sculpturing of the head, like that of most of the other parts, exceedingly dense and fine, the entire head viewed from in front being dull and opaque owing to its micro-

scopic granular surface (a little suggestive of the striking surface of a matchbox) that is utterly devoid of shiny interspaces; the sculpturing somewhat finer on the genal area, especially on its lower one-third, this area being somewhat shiny. The scape about as wide as the flagellum, which is fully three and one-half times as long as the scape. The head black with the following cream-colored maculations: a stripe from base to apex on the scape in front; a narrow stripe (a little wider below than above and sometimes a little emarginate at the level of the antennal socket) extending along the inner orbit of the eye almost to the level of the anterior ocellus; a small, rather trapezium-shaped spot in the supraclypeal area; the entire clypeus except for two short, narrow, subparallel, longitudinal, brownish to blackish stripes; the labrum (sometimes a little reddened). The basal half of the mandibles is apt to be blackish, the apical half reddish. The head with relatively few erect hairs and those silvery gray, being located on the lower margin of mandibles, lower one-third of genal area, labrum, and vertex, with appressed, very microscopic, silvery gray hairs of moderate density on upper two-thirds of genal area, front, sides of face, and to a less extent on the clypeus, producing a somewhat sericeous sheen over these parts.

THORAX: Sculptured like the head, exceedingly densely and finely granular to tessellate, with resulting opacity; only on the propodeum is the sculpturing a little less delicate and less crowded. The width of the mesonotum at its maximum, near the anterior margin, a little greater than its length, but the combined length of the mesonotum and scutellum distinctly greater than the maximum width of the mesonotum, about in the proportion of 7.5 to 6. The scutellum about twice as wide as it is long, its posterior rim slightly over-roofing the basal part of the propodeum, which extends backward for a distance a little greater than the length of the scutellum. The tubercles deflected somewhat from the horizontal to the vertical, in shape a little resembling a mussel shell. The erect hairs silvery gray, usually absent on the mesonotum (not so in two specimens from Lassance, Brazil, in which they are rather abundant anteriorly) but in the few males

before me well represented on the scutellum, where they occur both dorsally and fringing in horizontal growth the posterior margin. The mesonotum, mesopleura, and scutellum usually with a sericeous sheen due to their being covered densely with very microscopic silvery gray appressed hairs. The mesopleura, in the specimens from Lassance at least, have relatively short, erect, silvery gray hairs. The mesosternum with long, fairly dense, silvery gray hairs. The propodeum bare on the large dorsal and middle area but flanked on each side by a dense conspicuous patch of silvery gray to whitish tomentum. The thorax black with cream-colored areas as follows: the pronotum usually with a transverse stripe, medianly interrupted, along its posterior margin; the tubercles, a narrow stripe rimming continuously the sides of the mesonotum, the axillae, and the posterior margin of the scutellum, being of virtually uniform width except for a slight dilation on the axillae.

LEGS: With tessellation far more delicate than that of the other parts of the body. Brownish black, with a small pale spot externally at the base of each of the tibiae, largest on the hind tibiae (fig. 55B). The hairs silvery gray, but even fewer than in the conspecific worker, being absent from the regions where they are lacking in the worker and poorly developed, stunted, or even lacking in the areas where they are present in the worker. Erect hairs are present on the coxae, especially on the hind pair, and on the trochanters beneath. The femora have a microscopic fringe on their under side, but the fore and middle tibiae on their external face at least are devoid of erect hairs, although they have a silvery gray sericeous sheen. A few very stunted, stubble-like hairs occur along the anterior lateral margin of the hind tibiae (they become distinctly longer towards the apex of the joint), but there are even fewer hairs along the posterior lateral margin. The few erect hairs on the outer face of the metatarsi largely confined to the thin fringe along the posterior lateral contour of the joint; the hairs of the metatarsal brushes light golden. In addition to the sparse erect hairs, there are appressed pale hairs that give the joints viewed from certain angles a sericeous sheen.

WINGS: Uniformly clear and transparent,

iridescent. The venation and stigma brownish with the transverse cubital veins only very feebly demarked. The tegulae bright ferruginous with a fairly large cream-colored maculation anteriorly. The number of hamuli per hind wing is five in seven of the wings available for examination, but only four in the eighth wing, an average of 4.88.

ABDOMEN: Usually black to dark reddish black. When telescoped, which is usually the case, the dorsal aspect of the abdomen presents, as does that of the worker, a uniformly and densely sculptured surface without shiny interspaces. The bases of the tergites, when exposed, prove to be lightly sculptured instead of, as in the worker, completely smooth. Rather long silvery gray hairs fringe the apex of tergite 7, but the other tergites are without or virtually without erect hairs, although they have a sericeous sheen. The sternites and genitalia the same or virtually the same as those figured for *petropolis* (fig. 57). Sternites 1 and 2 with appressed or semi-appressed silvery gray hairs on their apical half, sternites 3 to 5 with much longer silvery gray hairs in the apical region. Sternite 4 medianly somewhat depressed and with a moderately deep, almost semicircular emargination at the middle of its apex, leaving two lateral lobes, each of which, measured along the thickened and hair-studded part of its apex, is about twice as wide as the maximum width of the median emargination. Sternite 5 also medianly depressed, with a deeper and wider emargination than that of sternite 4, the resulting lateral lobes hair fringed. Sternite 6 provided with a median spine that projects far beyond the flanking "shoulders." The tip of the median spine of sternite 6 somewhat knob-like, when viewed in profile, a character that could not be shown in the drawing of this sternite of *petropolis*, which shares the character, because of the position from which the specimen is viewed.

MEASUREMENTS: Length 3.75 to 4.5 mm.; width of thorax about 1.5 mm.; length of forewing, including tegula, 4 to 4.5 mm.

TYPE MATERIAL

Trigona (Paratrigona) lineata was described by Lepeletier from "Capitainerie de Goyan" (a misprint for Goyaz). The type specimens of *lineata* in the Muséum d'Histoire

Naturelle in Paris bear a rather more specific locality designation, namely, "Sud de la Capit^e de Goyaz."

DISCUSSION

Under the designation *lineata* there have been included from time to time things that should probably be assigned elsewhere. Say's *bilineata* is made a synonym of *lineata* by Ducke (now and then doubtfully) in his papers of 1910b, 1916, 1925, and 1945. However, Girard (1879, p. 723) considered *bilineata* as a bee approaching *Melipona scutellaris* in stature, and in an earlier paper (1876a, p. 193) had also classed it as a *Melipona*. Cockerell (1917, p. 127) interpreted *bilineata* as "extremely close to *T. bipunctata* Lep.," and my own impression is that it may be *Trigona (Partamona) testacea* variety *orizabaensis* Strand. Among specimens of stingless bees that have come to my attention from Mexico and Central America I have found none that are *lineata* and this, as well as the fact that Say's description of *bilineata* applies very inadequately to *lineata*, makes for caution in accepting *bilineata* (described from Mexico) as identical with *lineata* (described from Brazil). It is in my estimation doubtful whether indeed *lineata* extends northward even to the countries of South America that border the Caribbean, much less to the Central American states.

It is true that Ducke (1916, p. 104; 1925, p. 400; 1945, p. 80) included under *lineata* specimens from localities in the State of Pará, but I have never seen *lineata* as here delimited or specimens of the closely related *petropolis* from that state. On the other hand, there are before me specimens from Pará collected by Ducke himself that are *opaca*, an insect which Ducke does not take into cognizance in his monograph of the stingless bees of Brazil. Curiously enough, however, while his descriptions of *lineata* in 1916, 1925, and 1945 apply to *lineata* to the exclusion of *opaca* (for he particularly mentions the foreshortened scutellum of *lineata*), his earlier description (1902b, pp. 324-325) of *bilineata* (subsequently made by Ducke a synonym of *lineata*) unmistakably applies to what is in the present paper designated *opaca*. The only locality mentioned for *bilineata* in that earlier description, namely,

Pará (Belem), reappears among the locality designations for *lineata* in 1916, 1925, and 1945. It would seem likely that Ducke, while confining his descriptions in 1916, 1925, and 1945 to *lineata* as he then conceived it (and which in my estimation is the correct conception), nevertheless in his locality records of *lineata* included material that should have been assigned to *opaca*.

The colonies designated *lineata* by Cornelius (1875, pp. 184-185) and by Tomaschek (1879, pp. 582-587; 1880, pp. 60-65) were both established in stems of *Haematoxylon campechianum* that had been shipped to Europe, and the likelihood is that the bees came from the region about the Bay of Campeche, or at least not farther south than the Central American states, which is the range of *Haematoxylon campechianum*. There is strong doubt, therefore, whether the *lineata* of the articles by Cornelius and by Tomaschek is identical with the South American form. It is possible (but only barely possible) that what these authors refer to as *lineata* is *opaca*. Du Buysson (1901a, p. 106; 1901b, p. 155) described what he interpreted as the queen of *lineata* from Yucatan, but the mandibles of the worker as well as of the queen that he figures (1901b, pl. 5, figs. 9 and 10) do not suggest either *lineata* or *opaca*. Both figures show a mandible toothed merely on the inner one-third of the apex. Some doubt must exist also whether the specimens Friese (1908b, p. 93) reported from Salta, Argentina, are really *lineata* as here delimited. Friese alluded to them as follows: "The black form, but in small specimens only 5 mm.," but even 5 mm. would be excessively large for *lineata*, which is only unusually (and then due to distention of the abdomen) as much as 4.5 mm. in length.

Ducke (1916, pp. 104-105; 1925, p. 400; 1945, p. 80) stated that the abdomen of Amazonian specimens of *lineata* is black or brown, that of the central and south Brazilian specimens black or red. The first part of statement concerns, I think, primarily what in the present paper is interpreted as *opaca*. As for the south and central Brazilian specimens, those, at least, in the collections before me that have reddish abdomens seem to evidence other earmarks of the callow state.

There has been confusion between *lineata*

and *opaca*, yet the two are distinct not only in the character of their maculations but essentially in their plastic characters. The reader is referred to the key for details.

On the other hand, what is described in the present paper as *Trigona (Paratrigona) petropolis* is exceedingly close to *lineata* and, notwithstanding its wider scape, its structural identity in nearly all respects with *lineata* may prompt the feeling that it would be more correct to consider it a variety of *lineata* than an independent species.

It is difficult to decide whether among the bees here assembled as *lineata* there should not be further divisions into varieties. The specimens of maximum hairiness are from localities in the State of Minas Gerais, Brazil; those of much reduced hairiness from collecting sites in Argentina. Indeed the latter are not far removed from the hairless condition noted for variety *nuda*, but *nuda* has an additional claim to independence not shared by the Argentine specimens, thanks to its rather distinctive facial maculation.

Under the designation of *bilineata*, H. von Ihering reported (1903, p. 205) two subterranean nests, which may have been *lineata*, where Ducke (1916, pp. 104-105; 1925, pp. 400-401; 1945, p. 81) placed them. It is more likely, however, that they should be ascribed to *petropolis*. An unusually interesting nest site ascribed to an insect identified as *lineata* is that reported by Lucas (1889, pp. cvii-cviii), who stated that a colony was obtained in Minas Gerais, Brazil, from the deserted nest, pyriform in shape and covered with spiny processes, of the vespoid wasp, *Myrapetra scutellaris* White. R. von Ihering (1940, pp. 436, 880), in reporting the common name for the species, "jataí da terra," by virtue of its subterranean habits, noted also that nests have been seen within trees. The German-speaking population of southern Brazil is said to call *lineata* "Bodennest," the equivalent of ground nest (Ducke, 1925, p. 343).

DISTRIBUTION

Ducke (1916, p. 105; 1925, pp. 400-401; 1945, p. 80) listed among the regions where *lineata* has been collected, the Brazilian States of Pará, Pernambuco (on the authority of Marianno, 1911, pp. 81-82), Minas Gerais, Rio de Janeiro, São Paulo, and Santa Catha-

rina, as well as Bolivia and Argentina (on the authority of Friese). As Ducke (1902b, pp. 293, 324-325) designated as *bilineata* (subsequently made a synonym of *lineata*) specimens that are in the present paper considered to be a distinct species, namely, *opaca*, it is likely that his *lineata* of 1916, 1925, and 1945 is composite and that some of the states (particularly those in northern Brazil) he included in the geographic distribution may not have representatives of this species. Certainly the Pernambuco record, in so far as it rests on the citation from Marianno, is assignable not to *lineata* but to *opaca* as is evidenced by the description (under the designation *bilineata*) with which Marianno accompanies the record. It seems not unlikely, too, that *lineata* cited by Alfken (1930b, p. 9) from Iguassú, State of Bahia, and by the same author (1932b, p. 305) from the State of Pará is *opaca*.

Trigona lineata was described by Lepeletier from the "Capitainerie de Goyan [Goyaz]," which has a long north-south extension. The label on the type specimens is more specific, the designation being "Sud de la Capit^e de Goyaz." All of the Brazilian specimens of *lineata* before me are from the southern half of that country (this applies also to the closely related *petropolis*), and include some examples from Matto Grosso, a state which at the time Ducke wrote was not known to harbor the species.

The following localities are represented in the collections here reported upon:

BRAZIL: State of Minas Gerais: Bello Horizonte, Nov. 1-6, 1919 (Cornell Univ. Exped.); Lassance, Nov. 9-19, 1919, including males (Cornell Univ. Exped.); Diamantina, Nov. 14-18, 1919 (Cornell Univ. Exped.). State of Matto Grosso: Chapada (probably Sant' Anna do Chapada, near Cuyabá), Jan., March, April, male, Dec., male (H. H. Smith); Aquidauana, Dec. 11-13, 1919 (R. G. Harris).

ARGENTINA: San Juancito, Feb. 27, 1920 (Cornell Univ. Exped.); Jujuy, Feb. 11, 1920, including a male (Cornell Univ. Exped.); Cosquin, Sierra de Córdoba, March 1-9, 1920 (Cornell Univ. Exped.).

Trigona (Paratrigona) lineata variety *nuda* Schwarz

Trigona (Paratrigona) lineata variety *nuda* SCHWARZ, 1943b, pp. 4-6, figs. 2, 3.

Paratrigona lineata nuda, MOURE, 1944a, p. 71.
Trigona lineata variety *nuda*, SCHWARZ, 1944,
 p. 417.

WORKER

HEAD (FIG. 56): Structurally like typical *lineata*, black with the following areas yellow: a stripe from base to apex on the scape in front; a stripe (considerably wider below than above) extending along the entire inner orbit of the eye almost to the level of the anterior ocellus; a small trapezium-shaped maculation in the supraclypeal area; a tridentate figure occupying the lower one-half of the clypeus, the median element of the trident for the most part slender, up-pointing, shaped somewhat like a fool's cap, its extremity separated by an area of black from the supraclypeal maculation, the lateral elements of the trident wider, rather angular, their up-pointing extremity usually

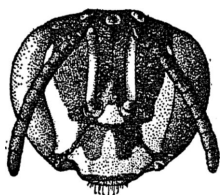


FIG. 56. Head of worker of *Trigona* (*Paratrigona*) *lineata* variety *nuda* Schwarz. Drawing by Shirley H. Risser.

approximating the rectangular; the labrum; the mandibles except for the dark basal prominence and the roseate to darkened apical extremity. The head almost completely devoid of erect hairs, which are confined to the lower one-third of the genal area, the inferior margin of the mandibles and the labrum; no, or only a negligible number of, stunted hairs on the vertex. In addition to these few erect hairs there is a sericeous sheen due to the presence over most of the head of dense, appressed, very microscopic, silvery gray hairlets. The upper two-thirds of the cheeks silvery gray pruinose.

THORAX: Structurally like typical *lineata*, but devoid of erect hairs on the mesonotum, scutellum, and mesopleura, having only appressed, sericeous, silvery gray hairs in these areas. The chitin black, with the following cream-colored to yellowish areas (corresponding with those of the typical variety): a transverse stripe (usually interrupted medially)

along the posterior margin of the pronotum supplemented usually by a much narrower transverse band along the anterior margin; the tubercles; a narrow stripe rimming continuously the sides of the mesonotum, the axillae, and the posterior edge of the scutellum, being of virtually uniform width except for a slight dilation on the axillae.

LEGS: With a maculation at the base of the outer face of all the tibiae, as in typical *lineata*. The hairs few, silvery gray, and distributed as in the typical variety.

WINGS: Uniformly clear and transparent, iridescent. The venation and stigma fuscous to black, with the transverse cubital veins fairly well demarked. The tegulae ferruginous with a cream-colored maculation anteriorly. The number of hamuli per lower wing usually five, rarely six, very exceptionally seven. Of 142 wings examined, 131 had five hamuli, 10 had six hamuli, and one had seven hamuli, an average of 5.08.

ABDOMEN: Black, structurally and in the absence of erect hairs on the tergites like typical *lineata*.

MEASUREMENTS: Length 3.5 to 4.5 mm.; width of thorax about 1.5 mm.; length of forewing, including tegula, about 4.5 mm.

QUEEN

Unknown.

MALE

Unknown.

TYPE MATERIAL

The entire type material of the variety *nuda* was collected in the Chanchamayo Valley of Peru, although the specimens were obtained from four different nests. The holotype and numerous paratypes are in the American Museum of Natural History.

DISCUSSION

The present variety, structurally like *lineata*, is characterized by the paucity of hairs that is associated with *opaca* and varieties of *opaca*. It can be separated from typical *lineata* by the absence of erect hairs on the scutellum and mesopleura, typical *lineata* being more or less hairy in both these areas. The clypeal maculation, too, is different, the median longitudinal stripe on the

lae largely reddish but usually somewhat sooty anteriorly and inwardly with frequently a dull yellow spot contiguous to the black area or two such spots, one anteriorly and one posteriorly, with a pupil between. Number of hamuli per lower wing five. Of 124 lower wings examined, 123 had five hamuli, and one had four hamuli with the stump of a fifth indicated.

ABDOMEN: Usually black, basal segment sometimes reddened. When telescoped, which is usually the case, the tergites present a uniformly tessellated to granular appearance devoid of shiny interspaces. When the abdomen is extended, however, the usually concealed basal areas of the tergites prove to be smooth and polished. The sternites somewhat more delicately and sparsely sculptured than the tergites. The tergites without erect hairs but usually with a sericeous sheen over their sculptured areas due to the presence of very microscopic appressed pale hairs. The ventral hairs as set down in the description of the subgenus.

MEASUREMENTS: Length 3.5 to 4.5 mm.; width of thorax about 1.5 mm.; length of forewing, including tegula, about 4.5 mm.

QUEEN

Unknown.

MALE

HEAD: Somewhat wider than long, in the proportion of about 8 to 7, nearly circular in contour, a little narrower than the distance between the outer rim of one of the tegulae and the outer rim of the other. The face very narrow. The distance from one eye to the other at their level of closest approximation (below) is a trifle less than one-half the length of the eye, whereas in the worker the shortest distance between the eyes is two-thirds of the length of the eye. The distance that separates the eyes at their level of closest approximation about as 3 is to 4 when compared with their divergence at the level just below the middle ocellus and about as 3 is to 6.5 when compared to the distance from the middle ocellus to the apex of the clypeus. The clypeus about two-thirds as long as wide, small, rather distinctly arched, hexagonal, the apex widely truncate along the middle and rather sharply receding at each side, the

apico-lateral angles approximating the rectangular and grazing the inner orbit of the eye. The labrum simple. The mandibles somewhat thumb shaped in outline, rather wide at the base, running to a point at the toothless apex, short, their tips barely meeting (not overlapping), the inferior margin convex in outline at the apex. The malar space surviving only as a tiny triangle near the outer angle of the base of the mandible, the inner angle of the base of the mandible being in contact with the rim of the eye. The distance between the lateral ocelli about twice the major axis of an ocellus, the distance between a lateral ocellus and the nearest compound eye barely less than, to equal to, the diameter of such an ocellus. The region behind the ocelli very slightly thickened. The sculpturing of the head, like that of most of the other parts, exceedingly dense and fine, the entire integument viewed from in front being dull and opaque owing to its microscopic granular surface (a little suggestive of the striking surface of a matchbox) that is entirely devoid of shiny interspaces; the sculpturing finer on the genal area, especially on the lower one-third of this area, which is feebly shiny. The scape with a diameter at its middle that is a little greater than the diameter of the flagellum; the flagellum fully three and one-half times as long as the scape. The head black with the following pale maculations: a stripe from base to apex on the scape in front; a narrow stripe (a little wider below than above) extending along the inner orbit of the eye almost to the level of the anterior ocellus; a small, rather trapezium-shaped spot in the supraclypeal area; a rather wide band along the anterior margin of the clypeus and conforming with its angulations (not infrequently the median portion of the band is non-existent with only two sundered bars, one in each lateral extremity of the clypeus surviving); occasionally a stripe bisecting the clypeus longitudinally and uniting with the band along the apex, but in most instances the clypeus is immaculate except for the apical band. The labrum is frequently more or less pale but is inclined to be sooty, and the mandibles are black or predominantly black except for their small yellowish apical tip. The head with relatively few erect hairs and these silvery gray; they are located

on the vertex, on the lower one-third of the genal area, and on the lower margin of the mandibles. In addition, there are silvery gray appressed hairs, densest on the upper two-thirds of the genal area but also on the front, sides of face, and clypeus, to which they impart a sericeous sheen.

THORAX: Sculptured like the head, exceedingly densely and finely granular to tessellate, with resulting opacity; only on the propodeum is the sculpturing a little less delicate and less crowded. The width of the mesonotum at its maximum, near the anterior margin, a little greater than its length but the combined length of the mesonotum and scutellum distinctly greater than the maximum width of the mesonotum, about in the proportion of 8 to 6.5. The scutellum about twice as wide as it is long, its posterior rim slightly over-roofing the basal part of the propodeum, which extends backward for a distance a little greater than the length of the scutellum. The tubercles deflected somewhat from the horizontal to the vertical, a little resembling in shape a mussel shell. The erect hairs silvery gray and negligibly few, absent from the mesonotum and the sides of the thorax, confined on the scutellum largely or wholly to the posterior rim, present only sparsely on the under side of the thorax and among the silvery gray to whitish tomentum at each side of the bare middle region of the propodeum. The mesonotum, mesopleura, and scutellum with very fine, dense, microscopic, appressed silvery gray hairs that impart to these areas a sericeous sheen. Thorax mainly black (but invaded by brown in callow specimens). A transverse pale stripe over the posterior half of the pronotum to the inclusion of the tubercles. A narrow pale stripe along each side of the mesonotum almost from the base to the inclusion of the axillae (where the stripe is slightly widened); a pale stripe (disconnected with the lateral stripes) along the posterior margin of the scutellum.

LEGS: With tessellation far more delicate than that of the other parts of the body. Reddish brown (but it is likely that the relatively light coloration is due to a callow condition) with a pale spot externally at the base of each of the tibiae (largest on the hind tibiae) and usually a pale spot, though

smaller, also at the apex of the tibiae (it is probable that these apical maculations, as are the pale yellow metatarsi, are indicative of the callow condition of the specimens rather than representative of the fully matured male insect). The legs almost wholly devoid of erect hairs, and even when these hairs occur, they are short and inconspicuous. There are a few silvery gray erect hairs on the coxae, particularly on the hind pair, very short hairs of like hue on the trochanters beneath and extending fringe-like and even more microscopic along the under side of the fore and middle femora (but often so reduced as to be no longer traceable). There are usually also a very few silvery gray hairs at the apex of the under side of the middle tibiae, and a few stunted silvery gray hairs along the anterior lateral contour of the hind tibiae, these hairs becoming longer towards the apex of the joint. The fine hairs that constitute the brushes on the inner face of the metatarsi are virtually the only erect hairs on the metatarsi. There is a faint sericeous sheen due to the presence of appressed, pale, very microscopic hairs.

WINGS: Uniformly clear and transparent, iridescent. The venation and stigma brownish, with at least the first transverse cubital vein fairly clearly demarked, the second more feeble. The tegulae reddish but unevenly so, with often a pale spot vaguely traceable anteriorly and a darker area frequently posteriorly (but the coloration probably misleading on account of the callow condition of the specimens). Of 10 lower wings available for examination nine had five hamuli and one had six, an average of 5.10.

ABDOMEN: In all the specimens before me reddish brown rather than black (in this respect unlike the worker), but the coloration is probably due to a callow condition. The basal part of the tergites (usually concealed) has, in contrast to the polished condition of the worker in this area, somewhat the same density of sculpturing that characterizes the apical part. Rather long silvery gray hairs fringe the apex of tergite 7, but the other tergites are without erect hairs although they have a sericeous sheen. Venter structurally virtually identical with that of male *lineata*. Sternites 1 and 2 silvery gray sericeous on their apical half; sternite 3 and particularly

sternites 4 and 5 with much longer silvery gray hairs in the apical region. Sternite 4 medianly somewhat depressed and with a moderately deep, almost semicircular emargination at the middle of the apex, leaving two lateral lobes, each of which, measured along the thickened and hair-studded part of its apex, is about twice as wide as the maximum width of the median emargination. Sternite 5, also medianly depressed, with a

TYPE MATERIAL

Holotype (from Petropolis, Brazil), male allotype, and paratypes at Cornell University; paratypes at the American Museum of Natural History.

DISCUSSION

This species is exceedingly close to *lineata* Lepeletier for which it is easily mistaken, as

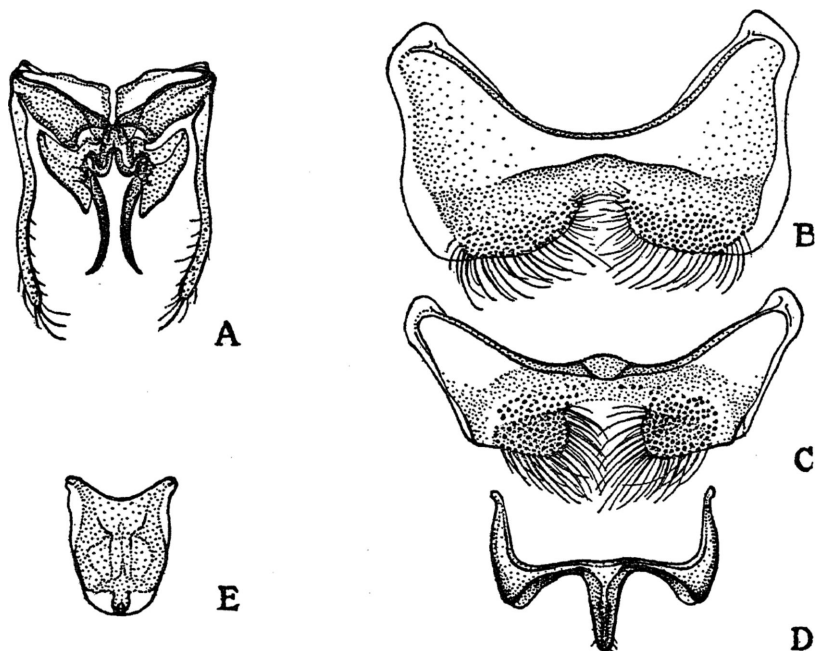


FIG. 57. Abdominal parts of male of *Trigona* (*Paratrigona*) *petropolis*, new species. A. Genitalia (chitinized parts only). B. Sternite 4. C. Sternite 5. D. Sternite 6. E. Sternite 7. All based on specimen from Jundiáhy, Brazil. Drawings by Shirley H. Risser.

deeper and wider emargination than that of sternite 4, the resulting lateral lobes hair fringed. Sternite 6 is equipped with a median spine that projects far beyond the flanking "shoulders." The tip of the median spine appears somewhat thickened, knob-like when viewed from the side, a character that could not be shown in the drawing in which the segment is viewed in the broad. (Fig. 57.)

MEASUREMENTS: Length 5 to 5.5 mm. (due largely to what seems a distortion of the abdomen); width of thorax about 1.5 mm.; length of forewing, including tegula, 4.5 to 4.75 mm.

it is approximately of the same size, of identical sculpturing, and shares many of the maculations of that species. As in *lineata*, it has a scutellum that is relatively short for a *Paratrigona*, extending backward only a little and leaving exposed the greater part of the propodeum when the insect is viewed from above. It departs structurally from *lineata* in having a scape of greater diameter. At its middle, where it is widest, the scape has a greater width than the flagellum, with which it is otherwise comparable in diameter. The scape is not, however, conspicuously swollen (as, for instance, in *prosopiformis* and

haeckeli) and even shows some variability in respect to width, specimens from Petropolis, for example, having a scape a little more robust than have specimens from Massaranduba-Blumenau. It may even be that because of this instability *petropolis* is more correctly considered a variety of *lineata* than an independent species, especially in view of the virtual identity of the sternites of the abdomen and the genitalia of the two forms. As has *lineata*, the present form has a trapezium-shaped supraclypeal maculation but, although the otherwise black scape of the worker is sometimes invaded by red anteriorly, especially basally, it usually lacks a clearly defined stripe such as characterizes the scape of the worker of *lineata*, and in other respects, too, the worker of *petropolis* shows a slightly greater degree of melanism than does the corresponding caste in *lineata*. The male, too, is of more limited maculation than is the male of *lineata*, as indicated in the key. Specimens of *petropolis* before me show an even greater paucity of hairs than specimens of typical *lineata*.

Presumably what H. von Ihering (1903, p. 205) referred to as *bilineata* is *petropolis*. One of two nests he obtained at Petropolis, the other at Itatiba. Both nests were located in the ground, the one at a depth of about half a meter, the other at the depth of 1 meter, but because the entrance passage was at an incline instead of vertical, the actual distance tunneled through the soil was in the first case 1 meter and in the second case 2 meters. Von Ihering made notation in the case of the first nest of a short, only slightly projecting entrance tube, thickly beset with bees. The second nest (the character of the first is not mentioned) consisted of combs, and the pollen and honey containers were placed in a half circle at the periphery of the nest. Von Ihering recorded the popular name of this bee as "jatahy da terra," bestowed apparently because of its habit in constructing subterranean nests. This name is the same as that applied also to *lineata* (Ducke, 1925, p. 343).

DISTRIBUTION

The specimens before me that are assignable to *petropolis* are all from southern Brazil:

BRAZIL: State of Rio de Janeiro: Rio de Janeiro, 1901; Tijuca, Oct. 17, 1919 (Cornell Univ. Exped.); Petropolis, Oct. 24-27, 1919, including holotype and male allotype (Cornell Univ. Exped.). State of São Paulo: São Paulo, 1897 (H. von Ihering); Jundiahy, Dec. 2, 1912, males, and Dec. 13, 1902. State of Santa Catharina: Massaranduba-Blumenau (K. Schmith).

Trigona (Paratrigona) opaca variety *opaca* Cockerell

? *Melipona lineata*, CORNELIUS, 1875, pp. 184-185 (identified by Gerstaecker).

? *Trigona lineata*, TOMASCHEK, 1879, pp. 582-587 (identified by "the director of the Zoological Museum in Vienna").

? *Trigona lineata*, TOMASCHEK, 1880, pp. 60-65 (identified by "the director of the Zoological Museum in Vienna").

Melipona bilineata, DUCKE, 1901, p. 65.

Melipona bilineata, DUCKE, 1902a, pp. 323, 419.

Melipona bilineata, DUCKE, 1902b, pp. 293, 324-325.

Trigona bilineata, MARIANNO, 1910d, p. 9.

Trigona bilineata, MARIANNO, 1911, pp. 5, 26, 40, 81-82, 115.

Melipona lineata, DUCKE, 1916, opposite p. 28, pp. 104-105 (in part).

Trigona opaca (lineata) subspecies? COCKERELL, 1917, p. 126.

Melipona lineata, DUCKE, 1925, pp. 343, 352, 400-401 (in part).

Melipona lineata, ALFKEN, 1930b, p. 9.

Melipona lineata, ALFKEN, 1932b, p. 305.

Trigona (Paratrigona) opaca variety *opaca*, SCHWARZ, 1938, pp. 448, 489-494, pl. 59, figs. C, C'.

Trigona (Paratrigona) opaca, BEQUAERT, 1943, p. 141 (identified by H. F. Schwarz).

Melipona lineata, DUCKE, 1945, opposite p. 24, pp. 80-81 (in part).

WORKER

DIAGNOSTIC CHARACTERS: Black with maculations. Scape narrow and rod-like, distinctly narrower than flagellum, the intermediate joints of which are distinctly wider than long. Facial maculations pale yellowish as follows: stripe anteriorly on scape, a narrow stripe along the inner orbit of the eye from the level of the middle ocellus to the antero-lateral angle of clypeus, thence inward and diagonally upward (sometimes interrupted) along the outer boundary of the side of the clypeus, a sometimes medianly interrupted transverse stripe that is expanded towards each of its lateral extremities border-

ing the apex of the clypeus, an arrow-shaped figure in the supraclypeal area, sometimes a narrow stripe extending briefly downward from the middle ocellus. Scutellum fully three-fifths as long as wide. Maculated tubercles vertical or nearly vertical in position. Pale yellow continuous stripe bordering sides of mesonotum and posterior margin of scutellum, slightly widened over axillae. Abdomen, when telescoped, uniformly dull above due to dense tessellation.

HEAD (FIG. 54C): Only a very little wider than long, in the proportion of about 8 to 7, the width barely greater than the distance from the outer rim of one of the tegulae to the outer rim of the other tegula. The face narrow, the distance between the compound eyes at a level just below the middle ocellus being only about two-thirds that from the anterior ocellus to the apex of the clypeus. The compound eyes slightly convergent below, the distance separating them at their level of closest approximation about as 4 is to 4.5 when compared to their divergence at the level just below the anterior ocellus. The clypeus about one-half as long as it is wide, gently arched, a little more elevated than the sides of the face, six sided, the apex widely truncate along its middle, more briefly but rather strongly receding to each side of the apical middle, the apico-lateral extremities subrectangular and separated from the nearest compound eye by less than the width of the flagellum. The supraclypeus about as prominent as the clypeus. The labrum slightly and rather evenly thickened, not tuberculate. The mandibles (fig. 54C1) overlapping each other, wider at their base and at their apex than they are at the middle; in perfect specimens with four teeth along their apical margin, of which the second (counting from the outside inward) is the widest and bluntest (but the teeth sometimes more or less worn away or united with one another by a septum of chitin). The malar space subtriangular, large on its outer half or more but distinctly shortened towards its inner extremity, where its length narrows down to only about half the width of the flagellum. The distance between the lateral ocelli (about twice the major axis of an ocellus) distinctly greater than that which separates each lateral ocellus from the nearest compound eye. The vertex somewhat thick-

ened and raised behind the ocelli. The sculpturing of the head, like that of most of the other parts of the body, dense and very fine, the entire aspect from in front being rather dull and opaque (though to a faint degree less opaque seemingly than the head of *lineata* and *petropolis*) owing to a microscopic granular surface; the sculpturing appears to be a little finer on the genal area, especially the lower one-third of that area, than on the face, with the result that these parts are feebly shiny. The scape narrow and rod-like, distinctly narrower than the flagellum and about one-half its length. The head black with the following pale yellowish maculations: a stripe from base to apex on the scape in front; a narrow stripe extending from approximately the level of the anterior ocellus downward along the inner orbit of the eye for the full extent of that inner orbit, at its lower extremity making a sharp angular bend inward and upward to extend part way along the outer boundary of the side of the clypeus and in such cases the maculation somewhat resembling a short-handled cane (but sometimes the connection between the parent stripe and its offshoot severed and in such cases the shorter stripe along the lateral outer boundary of the clypeus shrinking to a mere sundered spot); a transverse maculation (expanded towards each side, sharply narrowed inward of its lateral extremities and frequently with an interruption at the middle) near the apex of the clypeus; an upward-pointing angle (not a solid triangle or trapezium) in the supraclypeal area; a narrow stripe in some specimens (Pará, Prata, Igarapé-Assú) extending from the anterior ocellus part way down the frontal suture. Dull reddish are a narrow inconspicuous transverse stripe (sometimes obliterated by black) apicad to the irregular yellow band along the apex of the clypeus, the apical part of the mandibles, sometimes the labrum, and sometimes the third antennal joint below. The head virtually without erect hairs; these, occurring only on the lower one-third of the genal area, on the lower edge of the mandibles, and on the labrum, are silvery gray; the vertex is hairless. The upper two-thirds of the genal area is covered with appressed, silvery gray, microscopic hairs of only moderate density, and there is a seri-

ceous sheen over the face that is due to even more diminutive hairs of this character.

THORAX: Sculptured much like the head, exceedingly densely and finely granular with a resulting opacity that, if anything, is duller than that of the head. Only on the propodeum is the sculpturing a little less delicate and a little less crowded. The width of the mesonotum at its maximum, near the anterior margin, a little greater than its length (about as 6 is to 5); the combined length of the mesonotum and scutellum compared to the maximum width of the mesonotum about as 7.75 is to 6. The very flat scutellum fully three-fifths as long as it is wide, extending backward so far that, when the insect is viewed from above, it conceals most of the propodeum. The tubercles vertical or almost vertical in position, shaped somewhat like a mussel shell, with the upper extremity carinate. The thorax almost devoid of erect hairs, there being no such hairs on the mesonotum, mesopleura, or upper face of the scutellum; there are a few exceedingly short silvery gray hairs down growing on the posterior margin of the scutellum of some specimens, but even these are lacking in other specimens; on the mesosternum there are long silvery gray hairs rather densely represented. A sericeous sheen especially over the mesopleura due to the presence of microscopic silvery gray appressed hairs, and a dense, rather conspicuous patch of silvery gray to whitish tomentum at each side of the bare middle region of the propodeum. The thorax mainly black, with the following areas pale yellow: a transverse stripe (usually interrupted medianly) on the posterior half of the pronotum¹; the tubercles; a narrow band that rims continuously the sides of the mesonotum, the axillae, and the posterior margin of the scutellum, being of rather uniform width except for usually a slight dilation on the axillae.

¹ It may be noted that typical *opaca* lacks a supplementary transverse stripe along the anterior margin of the pronotum, as do the varieties *lundelli*, *anduzei*, *guatemalensis*, and *pacifica*, and the species *isopterophila* of limited maculation. The absence of this supplementary prothoracic stripe is to be noted also in the males, so far as known, not only of the forms just mentioned but also in the males of forms that in the worker have this supplementary prothoracic stripe.

LEGS: Sculptured more delicately than the other parts of the body, with usually the hind tibiae smooth and somewhat shiny towards the apex. Black (more rarely reddish brown), with well-developed, cream-colored to pale yellowish stripes (basally wider, apically narrower) from base nearly to the apex of the outer face of the fore and middle tibiae and along nearly the entire posterior margin of the hind tibiae (fig. 55C). The legs with a pale sericeous sheen, more especially on the hind femora, the outer face of the fore and middle tibiae, and the outer face of the middle and hind metatarsi, but with erect hairs few. Such erect hairs are silvery gray and are present on the coxae, particularly on the hind pair anteriorly; the trochanters beneath, particularly the middle and hind pair; the under side of the fore tibiae, but inconspicuous; the under side of the middle tibiae, where they are a little more in evidence; sparsely along the anterior and the posterior lateral contours of the hind tibiae, but the hairs on the anterior lateral contour tend to be a little the longer; a very few much longer hairs on the outer face of the hind tibiae; shorter along the posterior lateral contour of the fore and middle metatarsi. The metatarsal brushes tend to be light golden to reddish golden.

WINGS: Almost clear and transparent, iridescent. The venation and stigma fuscous to black, with the upper half of the first transverse cubital vein and the entire second transverse cubital vein clearly and fairly strongly demarked. The tegulae dark reddish to brownish with a pale yellow maculation anteriorly and a concolorous maculation also at the base of the wing. The number of hamuli per lower wing usually five. Of 40 wings examined, 39 had five hamuli and one had six hamuli, an average of 5.03.

ABDOMEN: Black to sometimes somewhat deep reddish black. When telescoped, which is usually the case, the tergites present a densely and uniformly sculptured surface devoid of shiny interspaces. When the abdomen is distended, however, the usually concealed basal areas of the tergites prove to be polished. The sternites a little more lightly sculptured than the tergites, and even the tergites not quite so densely opaque seemingly as the thorax. The dorsal aspect of the abdomen devoid of erect hairs but the ter-

gites with a sericeous sheen over their sculptured areas due to the presence of very microscopic pale appressed hairs. The ventral hairs as described for the subgenus. The abdomen completely black to very dark reddish black.

MEASUREMENTS: Length 3.75 to 4.5 mm.; width of thorax 1.25 mm. to about 1.5 mm.; length of forewing, including tegula, about 4 mm.

QUEEN

Unknown. Du Buysson (1901b, p. 155) described what he considered the queen of *lineata*. This description might seem to belong here because of the frequent confusion between *lineata* and *opaca*, but unfortunately neither Du Buysson's text nor his accompanying drawing warrants the assignment of his queen to either of these forms as here interpreted.

MALE¹

HEAD: Somewhat wider than long, in the proportion of about 8 to 7, subcircular in contour, a trifle narrower than the distance between the outer rim of one of the tegulae and the outer rim of the other. The face very narrow. The distance from one eye to the other at their level of closest approximation (below) is less than one-half the length of the eye, whereas in the worker the shortest distance between the eyes is about two-thirds the length of the eye. The distance that separates the eyes at their level of closest approximation about as 2.75 is to 4 when compared with the distance between them at the level just below the anterior ocellus and about as 2.75 is to 6 when compared to the distance separating the anterior ocellus from the apex of the clypeus. The clypeus fully two-thirds as long as it is wide, small, rather distinctly arched, six sided, the apex widely truncate along the middle and rather sharply receding to each side, the apico-lateral angles approximating the rectangular and grazing the inner orbit of the eye. The labrum simple. The mandibles rather thumb shaped in outline, rather wide at the base, running to a blunt point at the edentate apex, rather short (when retracted, at most touching each

other at their apical tips, not overlapping), their inferior margin convex in outline towards the apex. The malar space surviving only as a tiny triangle near the outer angle of the base of the mandible, the inner angle of the base of the mandible being in contact with the rim of the eye. The distance between the lateral ocelli about twice the major axis of an ocellus; the distance between a lateral ocellus and the nearest compound eye not more, rather less than the diameter of an ocellus. The region behind the ocelli somewhat carinate. The sculpturing of the head, like that of most of the body parts, exceedingly dense and fine, the entire head viewed from in front being dull and opaque due to a microscopic granular surface (a little suggestive of the striking surface of a matchbox) that is utterly devoid of shiny interspaces; the sculpturing of the genal area only a trifle less strong than that over the front and extending almost undiminished in density to the apex. The scape barely wider than the flagellum and about one-fourth its length. The head black with the following areas yellow: the scape from base to apex in front; a narrow stripe (a trifle wider below than above and with an emargination at the level of the antennal sockets) that extends upward along the inner orbit of the eye almost to the level of the anterior ocellus; a solid, nearly equilateral triangle in the supraclypeal area; the entire clypeus except for two short, faint, subparallel, longitudinal stripes of brown on the upper half of the clypeus; the entire mandible except for a narrow black stripe along the basal boundary and feeble reddening of the apical tip. The labrum cloudy reddish, the antennal sockets and the flagellum below reddish. The head with relatively few erect hairs and those, silvery gray, located on the apical half of the inferior margin of the mandible, lower one-third of genal area, and vertex, with appressed, very microscopic, silvery gray hairs on the upper two-thirds of the genal area, where they are dense, on the front, sides of face, and sparsely on the clypeus, producing a somewhat sericeous sheen.

THORAX: Sculptured like the head, exceedingly densely and finely granular to tessellate, with resulting opacity. Only on the propodeum is the sculpturing a little less deli-

¹ Description based on a cotype from Tabernilla, Canal Zone.

cate and less crowded. The maximum width of the mesonotum (near the basal margin) about equal to the length of the mesonotum, but the combined length of the mesonotum and scutellum exceeds the maximum width of the mesonotum in the proportion of about 8.5 to 6.5. The very flat scutellum fully three-fifths as long as it is wide, extending backward so far that, when the insect is viewed from above, the scutellum conceals most of the propodeum; the posterior margin of the scutellum almost semicircular with a nick-like, very feeble emargination at its middle. The tubercles vertical or almost vertical in position, shaped somewhat like a mussel shell, with the upper extremity carinate. The thorax almost devoid of erect hairs, there being no such hairs on the mesonotum, mesopleura, or upper face of the scutellum; there are a few silvery gray hairs down growing from the under side of the scutellum, particularly along the under side of its posterior margin. A sericeous sheen, due to the presence of microscopic, silvery gray, appressed hairs, on the mesonotum and especially the mesopleura, and a dense rather conspicuous patch of silvery gray to whitish tomentum at each side of the bare middle region of the propodeum. Mainly black but with the following pale yellow maculations that accord with those of the conspecific worker: a transverse stripe (medianly interrupted) along the posterior half of the pronotum; a narrow band that rims continuously the sides of the mesonotum, the axillae, and the posterior margin of the scutellum. The tubercles also maculated.

LEGS: With tessellation far more delicate than that of the other body parts. Brownish black to black with well-developed, cream-colored to pale yellowish stripes (basally wider, apically narrower) from base nearly to the apex of the outer face of the brownish ferruginous fore and middle tibiae and along posterior margin of the hind tibiae, virtually duplicating the markings of the conspecific worker. The fore metatarsi also with a pale stripe. The hairs silvery gray and scant, absent from areas where they are lacking in the conspecific worker and poorly developed, stunted, or even lacking in the areas where they are present in the worker. A few erect hairs occur on the hind coxae; very short

tomentum is present on the trochanters beneath; a microscopic fringe extends down the under side of the femora; the posterior face of the fore and middle femora and both the anterior and posterior face of the hind femora have, as has the external face of the tibiae, a more or less silvery gray sericeous sheen due to the presence of microscopic appressed hairs. There are a few erect hairs on the under side of the middle tibiae near the apex but, in the single specimen at least on which this description is based, there is not even a feeble representation of hairs along the posterior lateral contour of the hind tibiae and almost as complete an absence of hairs from the anterior lateral contour. A few hairs on the outer face of the anterior metatarsi but the outer face of the middle and hind metatarsi with only microscopic appressed hairs; the hairs on the inner side of the metatarsi for the most part silvery gray.

WINGS: Almost clear and transparent, iridescent. The venation and stigma fuscous to black, with the transverse cubital veins rather clearly and sharply demarked. The tegulae dark reddish to brownish with a pale yellow maculation anteriorly and a colorous maculation also at the base of the wing. The number of hamuli per lower wing five in the two specimens examined.

ABDOMEN: Black. When telescoped with the bases of the segments concealed, the dorsal aspect of the abdomen, like that of the worker, presents a densely and uniformly granular surface without shiny interspaces. Rather long silvery gray hairs fringe the apex of tergite 7, but the other tergites are without erect hairs although they have a sericeous sheen. The apical contour is flanked at each of its lateral extremities by a long, apically incurved slender tuft of hairs. The sternites for the most part with only short, silvery gray hairs, but long hairs fringing sternite 5. For the structure of the sternites and genitalia, see figure 58.

MEASUREMENTS: Length about 4.5 mm.; width of thorax about 1.5 mm.; length of forewing, including tegula, about 4 mm.

TYPE MATERIAL

Described from male specimens taken at Tabernilla in the Canal Zone. The holotype is in the United States National Museum and

a cotype is in the American Museum of Natural History.

DISCUSSION

Cockerell based *opaca* on the male. There is before me a series of males and a worker from Muzo, Colombia, but even without this definite association one would be inclined to

Ducke (1916, p. 104; 1925, p. 400; 1945, p. 80) made *bilineata* a synonym of *lineata*. But *bilineata* Say, whatever it may have been, and I believe it to be *Trigona* (*Partamona*) *testacea* variety *orizabaensis* Strand, cannot in my estimation be made to fit the insects here assigned to *opaca*, because, brief as is Say's description, it makes clear that the

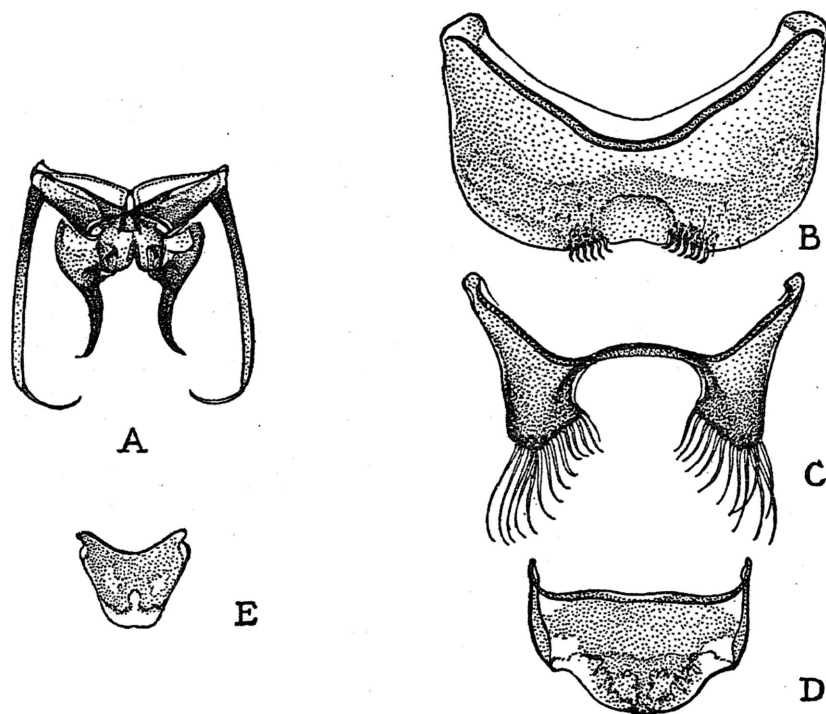


FIG. 58. Abdominal parts of male of *Trigona* (*Paratrigona*) *opaca* variety *opaca* Cockerell. A. Genitalia (chitinized parts only). B. Sternite 4. C. Sternite 5. D. Sternite 6. E. Sternite 7. All based on a cotype from Tabernilla, Canal Zone. Drawings by Shirley H. Risser.

place both male and worker in the same species and variety because of the similarity of their structure and of their maculation with allowance for sexual differences. Indeed, before this confirmatory evidence was obtained I had associated male and worker even though from different localities.

The workers here interpreted as *opaca* are undoubtedly the same insect that Ducke (1902b, pp. 324-325) designated *bilineata* Say. Before me is even a specimen collected by Ducke himself in Pará in 1902, which was identified by Friese as *bilineata*. Subsequently

clypeus has "two rather broad lines" while in true *opaca*, as here interpreted, the worker has only a transverse maculation apically on the clypeus. Indeed, while this maculation is a very superficial character, it offers an easy way of differentiating the worker of *opaca* from that caste in *lineata*, which always has a vertical stripe bisecting the clypeus. The maculation of the clypeus of the worker of *opaca* is suggestive rather of that in *impunctata*, to which in other respects *opaca* is rather less closely related than it is to *lineata*.

In addition to the typical variety of *opaca*

there are several other varieties to which recognition is given in the present paper. It is possible that additional forms should be separated. Thus even among the specimens that have been retained in typical *opaca* there is some variability, notably in the case of a stripe down the front of the worker, which is less developed in some specimens than it is in others, and may even be wholly lacking. All of the specimens before me from the State of Pará have such a stripe, while all of the specimens from British Guiana that I have had occasion to examine are without it. Possibly the evidence points to the existence of geographic races separable on the presence or absence of the frontal stripe; further specimens are desirable for the light they may throw on this surmise.

Although typical *opaca* is readily distinguishable from *lineata*, with which it has been confused from time to time, by the different character of its maculations, it is separated from it even more fundamentally by its structure, as is indicated in the key.

The reasons that have prompted me, although with misgivings, to include in the synonymy of *opaca* several references to *lineata* are set forth in the discussion and the distribution of *lineata* (pp. 363-364).

Although several instances have been reported of the erection of *Trigona* nests in the colonies of termites, the presence of these bees in the nests of ants, which ordinarily are rated among their worst enemies, is one to evoke wonder. Such a record has been contributed by Bequaert (1943, p. 141), who obtained the present species from a nest in a colony of *Dolichoderus* (*Monacis*) *bispinosus* at Muzo, Department of Boyacá, Colombia. According to Bequaert the *Dolichoderus* colony was located in a nest constructed in a bush about 5 feet above the ground. The nest was woven, and woven closely, of a fibrous material apparently derived from some plant, not, as are the nests of *Camponotus senex*, which also harbor colonies of stingless bees,¹ out of silk supplied by the larvae of the ants. In the opinion of the late William Morton Wheeler the nest occupied by the

Dolichoderus bispinosus colony was a nest that this aggressive ant had usurped from some other species, possibly an *Azteca*. Yet the colony of *Trigona* (*Paratrigona*) *opaca*, also at home in this usurped nest, was "seemingly on friendly terms with the *Dolichoderus*."

It may be that the association of *Trigona opaca* with *Dolichoderus bispinosus* is occasional rather than habitual, or is local and not general. At any rate, Marianno (1911, pp. 81-82) under the designation of *bilineata* recorded *opaca* as nesting in trees or in the crevices of old walls, instancing two such nests in his own house. Marianno challenged the statement of H. von Ihering (1903, p. 205) to the effect that the bee is ground nesting, asserting that its mandibles are too small to construct nests of a length of as much as 1 or 2 meters in the soil such as von Ihering recorded. However, when von Ihering commented on *bilineata*, it is almost certainly *petropolis* that he had before him, for one of his subterranean nests was obtained at Petropolis, whereas Marianno's bee was, judging from Marianno's accompanying description, *opaca*. I have personally never seen an *opaca* from southern Brazil, and the extension of its range to this area is somewhat puzzling. Marianno's description is in most respects a transcript of Ducke's description of *bilineata* (1902b, pp. 324-325).

From the nest of *Dolichoderus* (*Monacis*) *bispinosus* that housed the colony of *Trigona* (*Paratrigona*) *opaca* two myrmecophilous beetles were bred: one a paussid, *Homopterus steinbachi* Kolbe; the other a cremastochilid of the genus *Genuchinus* (according to A. Reichensperger).

While it is only very remotely possible that the bee that Tomaschek designated *lineata* was *opaca*, the floral records which Tomaschek supplied (1879, pp. 582-587) are summarized for such interest as they may have: *Haematoxylon campechianum* Linnaeus (doubtfully included on the basis of the pollen that survived the journey), wild grape, *Veronica speciosa* Cunningham. To these doubtful records may be added with more certainty *Miconia minutiflora*, which according to Ducke (1902a, p. 323) is frequently visited by "*bilineata*."

¹ See the Introduction to this paper (pp. 15-16) for an account of this and other instances of the association of stingless bees with ants.

DISTRIBUTION

Described from the Canal Zone. Represented in British Honduras, Guatemala, Colombia, Peru, British Guiana, and at least the State of Pará, Brazil. Marianno (1911, pp. 81-82), who describes this species under the misapprehension that it is Say's *bilineata*, lists not only Pará but also São Paulo and Pernambuco as states in which the bee occurs. Among many specimens of *Trigona* from southern Brazil I fail to find this species. The specimens in the collections before me are from the following localities:

BRITISH HONDURAS: Belize.

GUATEMALA: Department of Alta Vera Paz: Cacao, Trece Aguas, April 25 (Schwarz and Barber).

BRAZIL: State of Pará: Pará, April, 1902 (Ducke), and without date (Baker); Igarapé Assú, June 26, 1919, June 27, 1919, and July 15, 1919 (H. Parish); Prata, July 2-10, 1919 (H. Parish).

BRITISH GUIANA: Kartabo, July 27-29, 1924 (J. F. W. Pearson); Essequibo River, Moraballi Creek, Aug. 28, 1929 (Oxford Univ. Exped.).

COLOMBIA: Department of Boyacá: Muzo, 900 meters, 1936, from a nest located in a colony of *Dolichoderus bispinosus* (J. Bequaert).

PERU: El Campamento, Colony of the Perené, June 18, 1920 (Cornell Univ. Exped.).

Trigona (Paratrigona) opaca variety
lundelli Schwarz

Trigona (Paratrigona) opaca variety *lundelli*
SCHWARZ, 1938, pp. 448, 494-495.

WORKER

Differs from the worker of *opaca* variety *opaca* only by having its maculations pure white instead of yellow. Of eight wings counted, seven had five hamuli and one had six, an average of 5.17.

QUEEN

Unknown.

MALE

Unknown.

TYPE MATERIAL

Holotype (from British Honduras) and a few paratypes from that region and from Kartabo, British Guiana, are in the American

Museum of Natural History; additional paratypes are in the Museum of Comparative Zoölogy.

DISCUSSION

In its paler maculations this variety occupies somewhat the same relationship to typical *opaca* that *obscuripes* bears to typical *Melipona beecheii*.

In a vial containing specimens from Kartabo (W. M. Wheeler) were several fragments of the nest. The brood cells, measuring 2.25 by 3.25 mm., are arranged compactly and evenly in cells.

DISTRIBUTION

Known from British Honduras (without further locality record), where the specimens were collected in October and December, 1928, by C. L. Lundell, and from Kartabo, British Guiana, August 5, 1920 (W. M. Wheeler). In the latter locality, at least, occurs also typical *opaca*.

Trigona (Paratrigona) opaca variety
guatemalensis Schwarz

Trigona (Paratrigona) opaca variety *guatemalensis* SCHWARZ, 1938, p. 495.

WORKER

HEAD: Structurally like that of typical *opaca* except that the malar space is somewhat longer, at its shortest (near the inner angle of the base of the mandible) about as long as the flagellum is wide, in contrast to the mandible of the typical variety in which the corresponding measurement is only about one-half of the width of the flagellum. The apico-lateral extremities of the clypeus distant from the compound eye about the width of the flagellum. The maculations follow the general pattern of those of typical *opaca* but are more subdued and semi-extinguished. Thus the maculation that in the typical variety extends transversely close to the apex of the clypeus is obliterated or barely traceable along its narrowed middle portion, with the result that only the enlarged lateral extremities of this stripe appear clearly as more or less sundered spots. The band along the inner orbit of the eye is poorly developed and widely severed from the brief maculation along the outer boundary of the

sides of the clypeus. The up-pointing angular maculation in the supraclypeal area dull and sometimes fragmentary. The stripe down the scape in front tends to be reddish to fulvous instead of, as in the typical variety, pale yellow, while the under side of the flagellum, which in typical *opaca* tends to be black like the upper side, is distinctly reddish in *guatemalensis*. There is no evidence of a maculation below the middle ocellus such as characterizes some specimens included in typical *opaca*. A very few short, erect, pale hairs on the vertex in addition to the hairs noted for the typical variety.

THORAX: Like that of typical *opaca* except for the somewhat more restricted maculations. The transverse stripe on the pronotum inconspicuous and sometimes even absent. The tubercles maculated a little less fully. The bordering stripe along the sides of the mesonotum fails (contrary to the condition in typical *opaca*) to reach the extreme base of the mesonotum, and is terminated (again contrary to the condition in typical *opaca*) at the apex of the axillae, the narrow stripe rimming the posterior rim of the scutellum not being confluent with (as is the case in typical *opaca*), but distinctly separated from, the maculation on the axillae.

LEGS: Like those of typical *opaca* except that the maculations on the external face of the several tibiae are not stripe-like but have shrunk to a spot at the base.

WINGS: Much like those of typical *opaca*, almost clear and with fuscous to black venation and stigma. The transverse cubital veins even more strongly demarked than in typical *opaca*, the lower as well as the upper half of the first transverse cubital vein and the entire second transverse cubital vein being rather exceptionally emphatic for a meliponid bee. The tegulae deep brownish to blackish and without a pale yellow maculation (such as is present in typical *opaca*) or a concolorous spot at the base of the wing. The number of hamuli per lower wing usually five. Of 70 lower wings examined, 66 had five hamuli, three had four hamuli, and one had six hamuli, an average of 4.97.

ABDOMEN: As in typical variety.

MEASUREMENTS: Length 3.75 to 4.25 mm.; width of thorax about 1.5 mm.; length of forewing, including tegula, about 4 mm.

QUEEN

Unknown.

MALE

Unknown.

TYPE MATERIAL

The holotype from Chiquimulilla, Guatemala, and several paratypes from the same region are in the American Museum of Natural History. One paratype, also from Guatemala, is in the collection of J. Bequaert.

DISCUSSION

Although in this paper structural differences have in general been given specific recognition, it is sometimes difficult to evaluate a single structural difference when in all other plastic characters two insects are alike and approximate each other in the fundamental pattern of their maculations. Such a case is presented by *guatemalensis* in its relations to typical *opaca*. It has seemed preferable, in view of the relative insignificance of the structural difference, to consider *guatemalensis* a variety of *opaca* rather than an independent species. The larger malar space is shared by *guatemalensis* with *ornaticeps* and *anduzei*. The reader is referred to the discussion of *anduzei* for resemblances and differences between *guatemalensis* and *anduzei*.

DISTRIBUTION

All of the specimens except one on which *guatemalensis* is based were collected in March, 1923, by René Lichy at Chiquimulilla, Santa Rosa, Guatemala, at 300 meters. The additional specimen was collected in February-March, 1931, by J. Bequaert at Santa Emilia Pochuta, Guatemala, at 1000 meters.

Trigona (Paratrigona) opaca variety *anduzei* Schwarz

Trigona (Paratrigona) opaca variety *anduzei*
SCHWARZ, 1943a, pp. 27-30, 34.

WORKER

HEAD (FIG. 59): Structurally like that of typical *opaca* but with slight differences: The malar space is somewhat longer, at its shortest (near the inner angle of the base of the

mandible) fully as long as the flagellum is wide, in contrast to the malar space of the typical variety in which the corresponding measurement is only about one-half the width of the flagellum. The apico-lateral extremities of the clypeus distant from the compound eyes by more than the width of the flagellum. The maculations of much more restricted extent than in the typical form and more nearly approximating those of variety *guatemalensis*. The maculation that in the typical variety extends transversely close to the apex of the clypeus is in variety *anduzei* usually represented only by two widely sundered, small, yellowish, elongate spots (one in or near

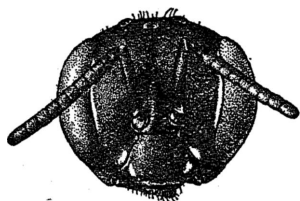


FIG. 59. Head of worker of *Trigona* (*Paratrigona*) *opaca* variety *anduzei* Schwarz. Drawing by Shirley H. Risser.

each of the antero-lateral extremities of the clypeus) that are at right angles each to a similarly shaped and concolorous spot located just outside the lateral boundary of the clypeus. In addition, along the apex of the clypeus are two small reddish spots¹ or a continuous red bar. Stripe along the inner margin of the eye of somewhat variable length but usually short, flanking as a rule only the middle region of the inner orbit. The supraclypeus fairly often immaculate but usually with two in-slanting small spots that form, in the rare instances in which they succeed in uniting above, an up-pointing arrowhead-like angle. The rest of the head coal black even to the inclusion of the scape and the flagellum; only the mandibles with a red stripe just before the apical teeth.

THORAX: With the scutellum a trifle shorter

than in typical *opaca*, although more produced than in the species *lineata*, the width of the mesonotum at the base when compared to the length of the mesonotum plus scutellum being about as 7 is to 8.75. In all the specimens of *anduzei* before me there is a well-defined nick at the middle of the posterior rim of the scutellum, which occurs also preponderantly in specimens of variety *guatemalensis* and is found occasionally in typical *opaca* and in other varieties of *opaca*. The pale yellow areas of the thorax of *anduzei*, more restricted than in typical *opaca*, are as follows: a medianly interrupted transverse stripe posteriorly on the pronotum; the tubercles; a stripe bordering the sides of the mesonotum from usually near the base of the mesonotum to the base of the axillae; sometimes a small, often onlyspeck-like maculation on the axillae but in many instances (53 cases of a total of 96 specimens examined) the axillae are wholly black²; a stripe rimming the posterior margin of the scutellum, although it fails to join with the stripe along the side of the mesonotum.

LEGS: Like those of typical *opaca* except that the maculations on the external face of the fore and middle tibiae, instead of being stripe-like, are reduced to a basal spot. The stripe on the hind tibiae, on the other hand, extends, as in typical *opaca*, along the posterior margin of the joint from the base almost to the apex.

WINGS: Almost clear, with pitch-black venation and stigma. The transverse cubital veins exceptionally strong for a stingless bee, comparable or almost comparable in the depth of their chitinization with the marginal vein. The tegulae and root of the wing black without pale maculations except for sometimes a brownish pupil on the tegulae. The number of hamuli per lower wing almost invariably five. Of 180 lower wings examined 176 had five hamuli and four had four hamuli, an average of 4.98.

¹ In a few exceptional cases of the 96 specimens before me there is also a small yellow maculation pyramided just above the two red spots, but in the vast majority of the specimens this yellow maculation is lacking. At the other extreme are a few specimens in which some or all of the maculations on or adjacent to the clypeus are lacking.

² One of the specimens of the total of 96 on which this description is based lacks not only the maculation on the axillae but the stripe along the sides of the mesonotum as well, although the stripe rimming the posterior margin of the scutellum is present as are the stripes on the pronotum and the maculation on the tubercles. The head, too, in this specimen is undermaculated, but the legs have the maculations usual for *anduzei*.

ABDOMEN: Like that of typical *opaca*.

MEASUREMENTS: More robust than typical *opaca* or any of the other varieties of *opaca*: length 3.75 to 4.5 mm.; width of thorax almost 2 mm.; length of forewing, including tegula, about 4.75 mm.

QUEEN

Unknown.

MALE

Unknown.

TYPE MATERIAL

All the specimens on which the description of *anduzei* is based are from Tabay, east Mérida, Venezuela. The holotype and a number of paratypes are being returned to P. J. Anduze; the remaining paratypes are in the American Museum of Natural History.

DISCUSSION

It is with some misgiving that this bee is made a variety of *opaca*. As the description will have indicated, it departs in more than one respect (notably in the greater length of its malar space and its slightly shorter scutellum) from the typical variety of *opaca*. However, it approximates in its slightly longer malar space such varieties of *opaca* as *guatemalensis* and *ornaticeps*, and in so many other respects it tends to link up with members of the *opaca* group that, tentatively at least, it seems best to retain it in that assemblage. Possibly the discovery of the as yet unknown male of *anduzei* may ultimately clarify its relationship more completely. If it has its correct place in the *opaca* complex, it is not only the most robust member of that group but also the most melanistic. It differs from all the other varieties of *opaca* in having wholly black antennae (scape as well as flagellum) and either wholly black or very much undermaculated axillae. From *guatemalensis*, possibly its nearest relative, it can be distinguished readily not only by these characters (in *guatemalensis*, for instance, the maculation on the axillae is wider, at least apically, than is the stripe along the lateral margin of the mesonotum) but by the maculation on the hind tibiae, which in *anduzei* runs from the base nearly to the apex along the posterior margin whereas in *guatemalensis*

there is only a basal spot. In *anduzei* the maculation of the thorax is discontinuous, the band rimming the hind margin of the scutellum not being confluent with the band along the lateral margin of the mesonotum. In all the other known varieties of *opaca* except *guatemalensis* the maculation in question is continuous.

DISTRIBUTION

All of the type material was collected in September 1942, by P. J. Anduze at Tabay, east Mérida, Venezuela, at 1760 meters.

Trigona (*Paratrigona*) *opaca* variety *ornaticeps* Schwarz

Trigona (*Paratrigona*) *opaca* variety *ornaticeps*
SCHWARZ, 1938, pp. 495-497, pl. 59, figs. D, D'.

WORKER

HEAD (FIG. 54D): Structurally like that of the typical variety but the malar space (fig. 54D1) is longer, the shortest distance between the eye and the mandible (measured near the inner angle of the mandible) being rather greater than the width of the robust flagellum, or the equivalent of about half the width of the mandible at the base, whereas in the worker of typical *opaca* the shortest distance is scarcely as much as half the width of the flagellum. As a result of the greater malar space, the apico-lateral angles are remote from the rim of the eye by at least the diameter of the flagellum. The ornamentation much more extensive and heavier than in typical *opaca*. Not merely the inner orbits of the eye but the outer orbits as well bordered by a yellow stripe of somewhat irregular outline that is wide below but narrows above. The stripes encircling the compound eyes are confluent with another yellow stripe of irregular thickness and somewhat zigzag contour that extends more or less brokenly across the vertex from the summit of one eye to the summit of the other. Extending from the middle ocellus downward to make contact with the supraclypeus is a yellow stripe that is strongly expanded (almost shovel-like) on its lower half. The supraclypeal maculation is a solid triangle of yellow, not merely an upward-pointing angle as in typical *opaca*. The clypeus wholly yellow except for two short, subparallel, vertical

stripes of blackish brown. The labrum yellow. The mandibles yellow except for their reddened apex, darkened four apical teeth, and black basal prominence. A yellow stripe on the scape in front. The sparse hairs silvery gray as in the typical variety and of the same limited distribution as noted for that variety.

THORAX: Shares with that of typical *opaca* the transverse yellow stripe across the posterior half of the pronotum, supplemented, however, by a very narrow transverse stripe anterior to this main stripe. As in typical *opaca* it has the vertical tubercles yellow, and a yellow stripe (a little wider possibly than that usual in typical *opaca*) rims continuously the sides of the mesonotum, the axillae, and the posterior margin of the scutellum. In addition to these maculations, the variety *ornaticeps* has the following thoracic maculations that are absent in typical *opaca*: a rather large irregular yellow maculation occupying the upper anterior half of the mesopleura (this spot has disintegrated into two spots in a specimen from El Volcan, Province of Chiriqui), another yellow maculation immediately below the hind wings, and a yellow spot sometimes on each side of the hairless central area of the propodeum (absent in specimen from El Volcan). The variety *ornaticeps* is fully as devoid of hair on the thorax as is the typical variety, and its sculpturing accords with that of the typical variety.

LEGS: In addition to the stripe on the outer face of the tibiae, extending from base virtually to apex in the case of the fore and middle pair, and along the posterior rim, also from base nearly to apex, in the case of the hind pair (maculations which are in accord with those of the typical variety of *opaca*) there is present in *ornaticeps* a yellow spot at the apex of the front femora. Except for these maculations, the color of the legs is mostly reddish to reddish brown in the type, predominantly black in the specimen from El Volcan. The smaller tarsal joints in both specimens are red. The silvery gray hairs of the legs accord in distribution with those of the typical variety.

WINGS: Almost clear and transparent, like those of typical *opaca*; the first transverse cubital vein, particularly the upper half of this vein, rather clearly defined, the second

transverse cubital vein more feeble. The venation and stigma brownish in the type specimen and black in the specimen from El Volcan. As in typical *opaca*, there is a yellow maculation anteriorly on the tegulae and a concolorous maculation at the root of the upper wing. The number of hamuli in each lower wing was five in the two specimens available.

ABDOMEN: In the type reddish yellow over much of the basal part of the first segment; remaining segments blackish. In the specimen from El Volcan blackish throughout. The abdomen proportioned and sculptured like that of typical *opaca*, with the erect hairs, as in that form, confined to the venter and of like color and relative length.

MEASUREMENTS: Length about 3.5 mm.; width of thorax about 1.5 mm.; length of forewing, including tegula, about 4 mm.

QUEEN

Unknown.

MALE

Unknown.

TYPE MATERIAL

The type, from Panama, is the property of Cornell University.

DISCUSSION

One is tempted to give specific rank to this insect, which differs not only in its maculations but also to a slight extent in its structure from typical *opaca*. The structural feature of most marked aberrant character (the length of the malar space) is, however, shared by *opaca* variety *guatemalensis*, which in most other respects is an almost exact counterpart of typical *opaca*, and also by the melanistic *opaca* variety *anduzei*. While structurally *ornaticeps* belongs with the *opaca* assemblage, in regard to its maculations it is rather strikingly like the structurally different *haeckeli*. Its thoracic maculations, at least, are also like those of *opaca* variety *lineatifrons*, and its facial maculations more nearly resemble those of *lineatifrons* than they do those of typical *opaca*. From *lineatifrons* the present insect differs, however, not only in the greater richness and extent of its

facial maculations and the presence of maculations (in the type at least) even on the propodeum, but also in having a more emphatic malar space.

DISTRIBUTION

The type is from the Changuinola District, Bocas de Toro, Panama, and was collected May 21, 1925, by J. C. Bradley. A second specimen was collected February 20, 1936, by W. J. Gertsch at El Volcan, Province of Chiriqui, Panama.

Trigona (Paratrigona) opaca variety *lineatifrons* Schwarz

Trigona (Paratrigona) opaca variety *lineatifrons* SCHWARZ, 1938, pp. 497-498, pl. 59, figs. E, E'.

WORKER

HEAD (FIG. 54E): Structurally like that of typical *opaca* but differently and more fully maculated. The clypeus with a yellow vertical stripe down its middle and a small triangle of yellow fitted into each of the anterolateral corners. The supraclypeal maculation a solid triangle of yellow, not merely an up-pointing angle. A yellow stripe extending from the anterior ocellus downward towards the supraclypeus, slightly and briefly expanded at its inferior end. A rather narrow stripe of yellow banding the eyes not merely along their inner orbits but along their outer orbits as well, the continuity of the encircling stripe briefly interrupted at the summit. A yellow stripe from base to apex on the scape in front, as in the typical variety. The mandibles, except for their black basal prominences, ferruginous, with their apex a brighter red. Labrum black.

THORAX: A yellow stripe along the sides of the mesonotum continuing without interruption along the axillae and the posterior rim of the scutellum, much like the bordering stripe that rims the thorax in the typical variety. The transverse stripe on the pronotum likewise comparable to that of typical *opaca*, but running parallel and anterior to this stripe there is in *lineatifrons* a narrow, supplementary stripe. The mesopleura, contrary to the condition in typical *opaca*, maculated on their anterior upper half with an irregular, somewhat W-shaped yellow figure, and a

yellow maculation also immediately below the hind wings. The tubercles maculated as in the typical variety.

LEGS: Brownish, maculated as in typical *opaca*.

WINGS: Almost transparent, with the venation and stigma brownish, the first transverse cubital vein with both upper and lower halves fairly distinct as is also the second transverse cubital. The tegulae reddish brown with a faded maculation anteriorly; the root of the wing with a pale yellow spot. Number of hamuli per lower wing five in the two specimens examined.

ABDOMEN: Deep brownish, with the characters noted in the description of typical *opaca*.

MEASUREMENTS: Length about 4.5 mm.; width of thorax approximating 1.5 mm.; length of forewing, including tegula, about 3.75 mm.

QUEEN

Unknown.

MALE

Unknown.

TYPE MATERIAL

This variety is based on a single specimen in the American Museum of Natural History that was collected August 30, 1902, by Ducke at Itaituba in the State of Pará, Brazil, and identified by Friese as *bilineata*.

DISCUSSION

The markings of the specimen to which the varietal name *lineatifrons* has been given seem to me sufficiently distinctive to separate it from typical *opaca*, with which it agrees structurally. The clypeal maculation resembles that of *lineata* rather than that of *opaca*, while in such respects as the band about the outer orbit of the eye and the supplementary maculations on the mesopleuron and metapleuron, the present insect allies itself with *opaca* variety *ornaticeps*.

DISTRIBUTION

Known only from Itaituba, State of Pará, Brazil.

Trigona (Paratrigona) opaca variety
pacifica Schwarz

Trigona (Paratrigona) opaca variety *pacifica*
SCHWARZ, 1943b, pp. 6-10, figs. 4, 5.

Paratrigona opaca pacifica, MOURE, 1944a, p.
71.

WORKER

HEAD (FIG. 60): Structurally like that of typical *opaca* but differs in its maculations. The clypeus with a rather anchor-like pale yellow maculation. The vertical shaft of the "anchor" rather wide, usually entire but in



FIG. 60. Head of worker of *Trigona (Paratrigona) opaca* variety *pacifica* Schwarz. Drawing by Alma Fröderstrom.

some specimens (especially those from Mariposa, Peru) occasionally fragmentary; the lateral extremities of the irregular transverse bar of the "anchor" very angular and much expanded. The supraclypeal maculation barely trapezium shaped, almost a solid triangle of pale yellow with only a very slight truncation at the top, not (as in typical *opaca*) rather arrow shaped but more nearly resembling the supraclypeal maculation of *lineata* and *petropolis*. No yellow stripe extending from the anterior ocellus downward as in varieties *lineatifrons* and *ornaticeps*, and even in some specimens here classed with typical *opaca*; the front is immaculate. A pale yellow stripe, as in typical *opaca*, extending from approximately the level of the anterior ocellus downward along the inner orbit of the eye for the full extent of that inner orbit. At its lower extremity it makes a sharp angular bend inward and diagonally upward to extend part way along the outer boundary of the side of the clypeus, suggesting in its configuration a short-handled cane. The scape with a yellow stripe in front.

THORAX: Like that of typical *opaca*, with the maculations duplicating those of typical *opaca*, except that the stripe that rims the

sides of the mesonotum from end to end and continues thence over the axillae and unbrokenly around the posterior margin of the scutellum is not any wider apically on the axillae than it is along the lateral border of the mesonotum. The tubercles and posterior half of pronotum maculated as in typical *opaca*.

LEGS: As described for typical *opaca*, with the cream-colored to pale yellowish stripes on the outer face of the fore and middle tibiae running from the base nearly to the apex of the joint and the stripe on the hind tibiae along the posterior margin of the joint also from the base nearly to the apex.

WINGS: As described for typical *opaca*, with a pale yellow maculation anteriorly on the tegulae and another at the root of the wing. Number of hamuli per lower wing usually five, more rarely six. Of 124 wings examined, 113 had five hamuli and 11 had six hamuli, an average of 5.09.

ABDOMEN: As described for typical *opaca*.

MEASUREMENTS: Length 3.5 to 4.5 mm.; width of thorax 1.25 to about 1.5 mm.; length of forewing, including tegula, about 4 mm.

QUEEN (GRAVID)

HEAD (FIG. 61A): Relatively smaller than that of the worker, about as wide as the mesonotum but not so wide as the distance between the outer rim of one of the tegulae and the outer rim of the other tegula. The face narrow, the distance between the compound eyes at a level just below the middle ocellus being only about two-thirds that from the anterior ocellus to the apex of the clypeus. The compound eyes almost parallel sided, the distance separating them at their level of closest approximation about as 5.5 is to 6 when compared to their divergence at the level just below the anterior ocellus. The clypeus about one-half as long as it is wide, gently arched, a little more elevated than the sides of the face, six sided, the apex rather widely truncate along the middle and rather strongly receding to each side of the apical middle, the apico-lateral extremities slightly subrectangular and separated from the nearest compound eye by somewhat more than the width of the flagellum. The supraclypeus about as prominent as the clypeus. The

labrum simple, rather slightly and evenly thickened. The mandibles (fig. 61) overlapping each other, wider at their base and at their apex than they are at their middle, their apex as clearly quadridentate as the apex of the mandible in the worker. The malar space longer than in the worker, at its shortest (towards the inner angle of the base of the mandible) about one-fourth longer than the flagellum is wide. The eyes not measurably smaller than those of the worker, a condition unusual in the Meliponidae. The distance between the lateral ocelli scarcely, if any, greater than that which separates a lateral ocellus from the nearest compound eye. The vertex somewhat thickened and raised behind the ocelli. The top of the supraclypeus and the anterior ocellus connected by a deep sulcus. The sculpturing of the head, like that of the thorax, dense and very fine, the entire surface being rather dull and approximately opaque owing to a microscopic granular surface, which is a little finer on the genal area than on the face. The scape somewhat more robust than in the worker, at least equal to the flagellum in width and about half as long. The head black but with maculations that are even rather more extensive than those of the covarietal worker. Thus the entire clypeus is rust colored to yellowish, the rust-colored areas occupying most of the clypeus except the apico-lateral extremities and the apical margin, which are pale yellow. There is a solid triangle of pale yellow on the supraclypeus. The stripe along the inner orbit of the eyes is expanded below (in the area between the clypeus and the eye), having an in-pointing extremity; the stripe tapers upward, ending slightly below the level of the anterior ocellus. There is a stripe (as in the worker) anteriorly from base to apex on the scape but (unlike the worker) the flagellum is bright ferruginous beneath. Unlike the condition, too, in the worker, the mandible of the queen is yellowish to roseate throughout except for the dark apical prominence and the blackish teeth. The labrum also is reddish, and the lower extremity of the genal area, as well as the malar space, is pale or largely so. The head devoid of erect hairs except on the labrum and along the lower margin of the mandible, the hairs in these areas being silvery gray to

ferruginous and long, those near the base of the mandible as long as, if not longer than, the mandible is wide. A sericeous sheen, more particularly over the upper half of the head, due to the presence of very microscopic, silvery gray hairlets.

THORAX: Sculptured much like the head, very densely and finely granular; the sculpturing on the propodeum a shade coarser and a trifle less crowded than that of the mesonotum. The thorax considerably wider than that of the worker. The width of the mesonotum at its maximum near the basal margin

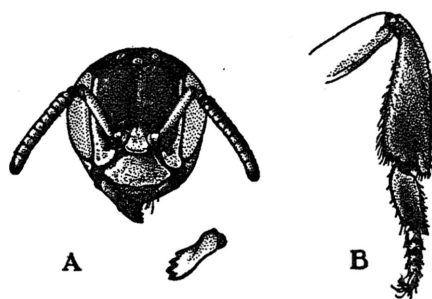


FIG. 61. Queen of *Trigona* (*Paratrigona*) *opaca* variety *pacifica* Schwarz. A. Head and mandible. B. Tibia, metatarsus, and small tarsal joints of hind leg. Drawings by Shirley H. Risser.

about equal to the combined length of the mesonotum and scutellum. The scutellum about three-fifths as long as its greatest width, but, unlike the condition in the worker, the robust propodeum is largely visible when the insect is viewed from above, being very inadequately covered by the scutellum. The tubercles vertical or almost vertical in position, shaped somewhat like a mussel shell, with the upper extremity somewhat carinate. The thorax devoid of erect hairs except for rather long ferruginous hairs fringing the scutellum posteriorly and rather long silvery gray hairs on the under side of the thorax. A sericeous sheen over the mesonotum, mesopleura, and scutellum due to the presence of very microscopic silvery gray hairlets. The silvery gray tomentum on the sides of the propodeum very short and inconspicuous, with a sericeous sheen. The mesonotum and scutellum black, the mesopleura and the pronotum anteriorly brownish black to brownish. The propodeum rust

colored. There are the following cream-colored to yellowish areas: a transverse stripe over the posterior half of the pronotum; the tubercles; a narrow band that rims continuously the sides of the mesonotum, the axillae, and the posterior margin of the scutellum, being of rather uniform width throughout, the part of the band on the axillae no wider than that part of the band along the sides of the mesonotum.

LEGS: More robust than those of the worker but of very limited and feeble sculpturing, which is traceable in the form of an exceedingly fine tessellation more especially on the outer face of the fore and middle tibiae and the anterior face of the hind femora, the general condition, even in these areas, approximating the smooth. The middle legs intermediate in length between the short fore legs and the long hind legs. The fore tibiae and the middle tibiae notably shorter than their femora, reversing the condition of the hind pair of legs in which the tibiae are distinctly longer than the femora, although not so long as the femora and trochanters combined. The hind tibiae (fig. 61B) subtriangular in outline, widest at apex, a little wider and longer by a third than the hind tibiae of the worker. Their anterior lateral contour almost straight to very feebly convex. Their anterior lateral contour almost straight to very feebly convex. Their posterior lateral contour without convexity except at the extreme base, being otherwise straight throughout and ending in a posterior apical angle. The apical contour rounded on the anterior two-thirds but emarginate on the posterior one-third. The outer face gently arched except near the apex, where it is briefly depressed. The inner face more strongly arched than the outer face and without a posterior rim. The hind metatarsi at their widest (near the base) a little more than half the width of the hind tibiae at their widest, tapering slightly towards the apex; the length of the hind metatarsus about that of the combined small joints of the tarsus. The outer face of the fore and middle tibiae, the anterior face of the hind femora, and the outer face of the metatarsi with a feeble sericeous sheen due to the presence of very microscopic, silvery gray hairlets. The erect

hairs few, short, and inconspicuous so that the general effect is one of nudity. There are a few silvery gray hairs on the coxae, trochanters beneath, fringing the under side of the middle femora, lower half of anterior margin of middle tibiae, and especially the lower half of the anterior margin of the hind tibiae. The inner face of the hind tibiae densely covered from base to apex with very microscopic, silvery gray hairlets. The metatarsal brushes light golden. In contrast to the black legs of the worker those of the queen are mainly fulvous, with black stripes, however, on the under side of the femora and cloudiness here and there also in other areas.

WINGS: In present specimen very much worn, their apical half missing, the surviving basal part clear and transparent. The venation more or less fuscous; the first and second transverse cubital veins entire and rather strongly demarked. The tegulae brownish with a large cream-colored spot anteriorly and a small spot inwardly and posteriorly; a large cream-colored maculation at the root of the wing. Hamuli destroyed in present specimen.

ABDOMEN: Very greatly distended and shapeless, much longer than the combined length of the head and thorax and also wider and thicker than either the thorax or the head. Its color, except for cloudiness on the basal tergite, fulvous throughout, contrasting with the black abdomen of the worker. Tergite 1 devoid of hairs and the second tergite nearly so except for the sides and narrowly and sparsely along the apex. The subsequent tergites with short pale dense hairs that are very slightly longer from tergite to tergite and on tergites 5 and 6, at least, have an almost velvety surface. Along with these hairs of uniform level are a few hairs of longer growth, especially on the apical half of tergite 5 and on tergite 6. A few short, erect, silvery gray hairs on the apex of the several sternites, those of sternite 1 being the longest. Sternite 6 almost entire, only feebly nicked at the middle of its apical contour.

MEASUREMENTS: Length 8 mm. (of which the abdomen alone accounts for about 5 mm.); width of thorax about 2.25 mm.; length of forewing, judging from the basal part surviving, actually somewhat longer

than that of the worker but, in relation to the much greater body size of the queen, proportionately smaller than the wing of the worker.

MALE

Scarcely to be differentiated from the male of typical *opaca*.

TYPE MATERIAL

The holotype (worker) and allotype (queen) from Valle de Chanchamayo, Peru, and paratypes from the same locality, from Mariposa, Peru, and from Tena, Ecuador, are in the American Museum of Natural History.

DISCUSSION

Very close to the typical form, from which it differs mainly in the fuller maculation of the clypeus and the supraclypeus of the worker and in the relative narrowness of the stripe on the axillae (wide at least apically in most of the varieties of *opaca*). The form *pacifica* tends to approach the reduction to absence of maculation on the axillae that is so marked in *opaca* variety *anduzei*.

In some of the specimens from Mariposa, Peru, the clypeal maculation, especially the central shaft of the "anchor," tends to be blurred, broken, or even sometimes absent. Such specimens also sometimes have the supraclypeal maculation slightly emarginate with black below. In all of these respects they resemble to some degree typical *opaca*, although usually they bear the earmarks of variety *pacifica* in having the stripe over the axillae unexpanded and no wider than the stripe on the mesonotum. As in the large series of *opaca* variety *anduzei*, so in this rather large series of *opaca* variety *pacifica* from Mariposa, Peru, the maculations are not completely stabilized.

Note the short joints of the antennae in the worker of *pacifica* by which this bee is readily separated from that caste of *lineata* variety *nuda* of very similar facial maculation.

Dr. W. Weyrauch, to whom I am indebted for the specimens from Peru, made note in his accompanying field observations that the specimens from Mariposa in that country were obtained from a nest built in an entanglement of roots of orchids on a tree trunk. But interesting as this nest site is, it

yields in significance to the other reported cases, all from San Ramon in the Valle de Chanchamayo of Peru, where that observer came upon at least three nests¹ of *pacifica* that had been established in the nests of birds. One of these *pacifica* nests (No. 157) was in a birds' nest made of straw. The second *pacifica* nest (No. 171) was in a birds' nest located on the limb of a tree. The third nest (No. 149) was attached to the dead limb of a tree at the time that the photograph reproduced herein (pl. 5, fig. 5) was taken. Weyrauch's field note, however, indicates that this bee colony was originally started in a birds' nest but that the material constituting the birds' nest was carried off progressively as the wax structure of the bees tended to expand. The bees' nest, measured externally, was 14 cm. wide and 14 cm. long. Within there were 10 brood combs which in descending order had, according to the calculations of Weyrauch, respectively the following diameters, all measured in centimeters: 3.5, 3.5, 5, 4.5, 5.5, 6, 7, 7.5, 6, 3. The cells containing the pupae of workers were 5 mm. long; the royal cells, 12 mm. long.

The use of birds' nests, occasionally at least, has been noted in the case of certain bumblebees of the Old World as well as of the New, including our own *Bombus vagans*. There are also a few such records for stingless bees (see Introduction, p. 17). The case of *pacifica*, however, is the only instance that has come to my notice where a *Trigona* has followed a similar odd selectivity not once but persistently. The fact that all three of the observed nests of this form in a given area were established in the nests of birds points strongly to a predilection, at least locally, for this type of nest site on the part of *pacifica*.

DISTRIBUTION

The variety *pacifica* is known as yet only from certain South American countries bordering the Pacific, as follows:

ECUADOR: Tena, March 24, 1923 (F. X. Williams).

¹ A fourth nest, No. 159, is likewise noted by Weyrauch as having been constructed in the nest of a bird on the limb of a tree. Unfortunately specimens from this nest did not reach me, but the probability is that they were *opaca* variety *pacifica*.

PERU: San Ramon, Valle de Chanchamayo, 800 meters, April 1, 1939, No. 149, No. 157, No. 171 (W. Weyrauch); Mariposa, near Huancayo, at 1200 meters, No. 135 (W. Weyrauch).

Trigona (*Paratrigona*) *prosopiformis* (Gribodo)

Melipona prosopiformis GRIBODO, 1893, pp. 259-260.

Melipona prosopiformis, DALLA TORRE, 1896, p. 582.

?*Trigona longicollis* FRIESE, 1903, pp. 360-361.

?*Trigona longicollis*, MARIANNO, 1911, pp. 115-116.

Melipona prosopiformis, DUCKE, 1916, opposite p. 28, pp. 103-104.

Melipona prosopiformis, DUCKE, 1925, pp. 343, 352, 399-400.

Trigona prosopiformis, SCHWARZ, 1932a, p. 259.

Trigona (*Paratrigona*) *prosopiformis*, SCHWARZ, 1938, pl. 58, figs. D, D'.

Paratrigona prosopiformis, MOURE, 1944a, p. 71.

Melipona prosopiformis, DUCKE, 1945, opposite p. 24, pp. 79-80.

WORKER

DIAGNOSTIC CHARACTERS: Black, with maculations. Scape notably swollen, at its widest (about the middle) twice the width of the flagellum; intermediate joints of flagellum about as long as wide. Facial maculations yellow and as follows: stout stripe on scape anteriorly, a stripe along the inner orbit of the eye that tapers upward to terminate near the level of the middle ocellus but is widened knob-like at its lower extremity, a more or less anchor-like figure occupying most of clypeus, a solid triangular figure in supra-clypeal area. Malar space very large at its outer extremity, but even at the narrow inner extremity it has a length almost equal to the width of the flagellum. Scutellum about three-fifths as long as it is wide. The maculated tubercles only slightly deflected from the horizontal to the vertical. A pale yellow stripe along the side of the mesonotum, widened over the axillae, and continued (usually after an interruption) along the hind margin of the scutellum. Abdomen, when telescoped, uniformly dull above owing to dense sculpturing.

HEAD (FIG. 62D): Barely wider than it is long¹ and almost circular, its width a trifle

¹ Friese (1903, p. 360) says of *longicollis*, which is a synonym of *prosopiformis*, that the head is longer than wide, but specimens, some of them with metatype

greater than the distance from the outer rim of one of the tegulae to the outer rim of the other tegula. The face narrow, the distance between the compound eyes at a level just below the middle ocellus being approximately two-thirds that from the anterior ocellus to the apex of the clypeus. The compound eyes hardly convergent below, the distance separating them below being just about the same as the distance separating them near the summit. The clypeus more than one-half as long as it is wide, gently arched, a little more elevated than the sides of the face, six sided, the apex widely truncate along its middle, more briefly but rather distinctly receding at each side of the apical middle, the apico-lateral extremities somewhat less than rectangular and separated from the nearest compound eye by more than the width of the flagellum. The supraclypeus about as prominent as the clypeus. The labrum slightly and rather evenly thickened, simple. The mandibles (fig. 62D1) overlapping each other, wider at their base and at their apex than they are at the middle; in perfect specimens with four teeth along the apical margin of the mandible, of which the second (counting from the outside inward) is the widest and bluntest (but the two outer teeth often not so clearly defined as the two inner, not infrequently more or less fused).² The malar space subtriangular, large on its outer half or more but distinctly shortened towards its inner extremity, where, however, it has a length barely less than the width of the flagellum. The distance between the lateral ocelli (about three times the diameter of an ocellus) distinctly greater than that

labels, received from Friese do not sustain this statement.

² It was doubtless because of this deceptive fusing of the outermost teeth that several of the descriptions fail to take cognizance of the quadridentate condition. Thus Gribodo (1893, p. 260) pronounced the mandibles to be without dentition and under this impression assigned his *prosopiformis* to *Melipona* although admitting that it had the stature and appearance of a *Trigona*. Friese (1903, p. 361) spoke of the edge of the mandible in his *longicollis* as virtually entire, or toothless. Even Ducke (1916, p. 103; 1925, p. 399; 1945, p. 79) described the mandibles as almost toothless. In spite of an occasional septum between the outermost teeth, the mandible when fully revealed usually shows the condition indicated in figure 62D1.

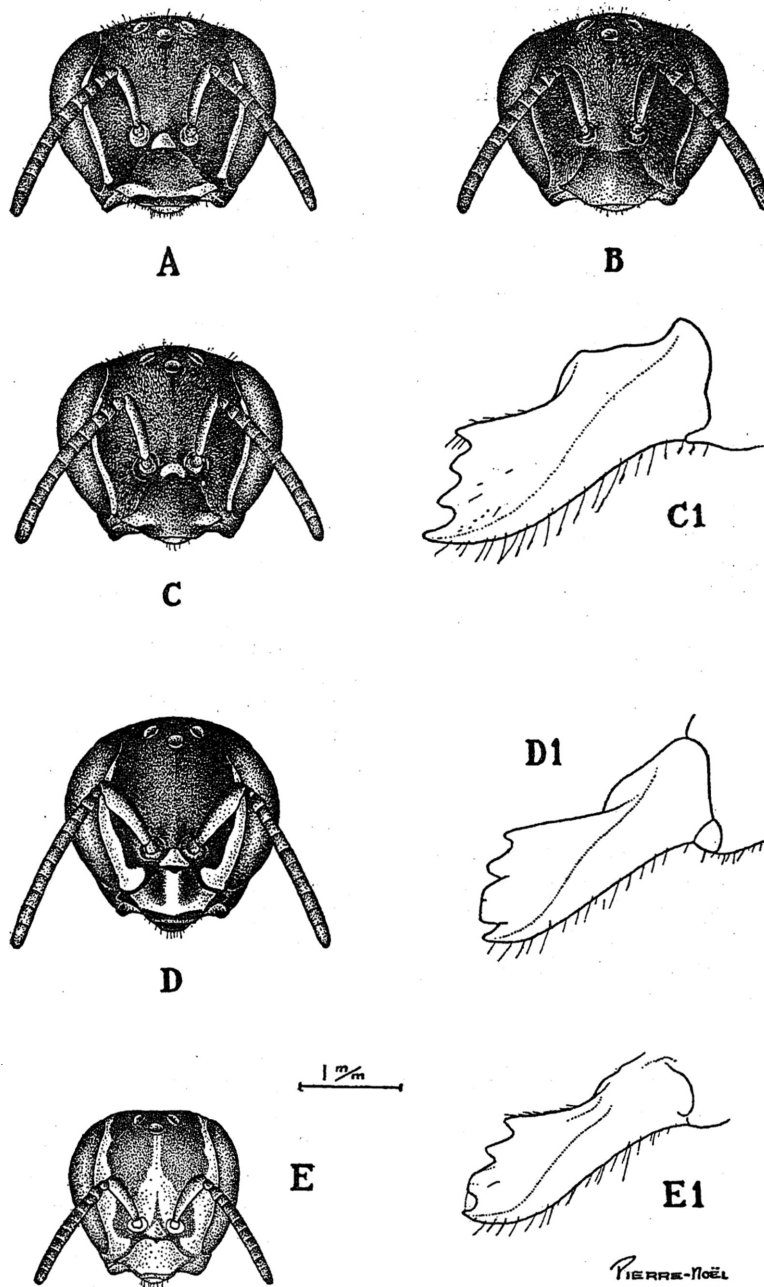


FIG. 62. A. Head of worker of *Trigona* (*Paratrigona*) *impunctata* (Ducke), fully maculated example. B. Head of worker of *Trigona* (*Paratrigona*) *isopterophila* Schwarz. C, C1. Head of worker and mandible, respectively, of *Trigona* (*Paratrigona*) *impunctata* (Ducke), undermaculated example. D, D1. Head of worker and mandible, respectively, of *Trigona* (*Paratrigona*) *prosopiformis* (Gribodo). E, E1. Head of worker and mandible, respectively, of *Trigona* (*Paratrigona*) *haeckeli* Friese. Drawings by V. Pierre-Noël.

which separates each lateral ocellus from the nearest compound eye (about twice the diameter of an ocellus). The vertex somewhat thickened and raised behind the ocelli. The sculpturing of the head, as is that of most of the other parts of the body, exceedingly dense and fine, the entire head, viewed from in front, being dull and opaque owing to its microscopic granular surface (a little suggestive of the striking surface of a match-box) that is utterly devoid of shiny interspaces. The sculpturing somewhat finer on the genal area, especially the inferior one-third of this area, which is sometimes faintly shiny. The scape very notably swollen; relatively slender at the base, it is much expanded towards the middle, its inner contour being strongly convex; at its widest it is nearly twice the width of the flagellum and about one-half the length of the flagellum. The head black with the following yellow maculations: a stout stripe from base to apex on the scape in front; a stripe along the entire inner orbit of the eye almost to the level of the anterior ocellus, tapering towards its upper extremity but decidedly widened inwardly at its lower extremity by a knob-like expansion; a stout vertical stripe down the middle of the clypeus from base to apex, bisecting a transverse stripe of irregular thickness (tending to be widest at its lateral extremities) that extends close to the apex of the clypeus, from which it is separated by a narrow band of black; a solid triangle in the supraclypeal area. There is in none of the specimens before me a longitudinal stripe just below the median ocellus such as characterizes some specimens of the closely related *opaca*. The labrum and the mandibles (except for a brief area of red just before the black teeth) are black. There is frequently a very narrow transverse line of red along the apex of the clypeus, and a half-ring of red often occurs on the under side of the second joint of the flagellum, which is otherwise black or at least dark. The head virtually without erect hairs. There are a few silvery gray hairs on the lower one-third of the genal area, fringing the inferior margin of the mandibles, and on the labrum; the vertex is devoid of erect hairs. The upper two-thirds of the genal area is covered with appressed silvery gray microscopic hairs of only moderate density,

and there is a sericeous sheen over the face that is due to even more diminutive hairs of this character.

THORAX: Sculptured like the head, exceedingly densely and finely granular, very opaque. Only on the propodeum is the sculpturing a little less delicate and a little less crowded. The width of the mesonotum at its maximum, near the anterior margin, a little greater than its length (in the proportion of slightly more than 7.5 to 6.5), the combined length of the mesonotum and scutellum compared to the maximum width of the mesonotum about as 9.5 is to 7.5. The very flat scutellum fully three-fifths as long as it is wide, extending backward so that, when it is viewed from above, it conceals or nearly conceals the propodeum (much as in *opaca*); the rounded hind margin of the scutellum in some specimens with a nick-like emargination at the middle. The tubercles only slightly deflected from the horizontal to the vertical (more nearly orientated like those of *lineata* and *petropolis* than like the vertically placed tubercles of *opaca*) and shaped somewhat like a mussel shell. The thorax almost devoid of erect hairs, there being no such hairs on the mesonotum, mesopleura, or upper face of the scutellum. A few very short silvery gray hairs are usually present on the under side (especially laterally) of the posterior rim of the scutellum and there are rather long silvery gray hairs on the mesosternum. A sericeous sheen especially over the mesopleura due to the presence of microscopic, silvery gray, appressed hairs, and a dense rather conspicuous patch of silvery gray to whitish tomentum at each side of the bare dorsal and middle region of the propodeum. The thorax mainly black but with the following maculations that are often a paler yellow than those of the head: a transverse stripe, medianly interrupted, along the posterior margin of the pronotum and a much narrower stripe along the anterior margin of the pronotum; likewise a stripe margining the sides of the mesonotum to the inclusion of the axillae, where it tends to expand slightly; a continuation of this stripe, usually after more or less of an interruption, along the posterior margin of the scutellum. The tubercles also maculated.

LEGS: More daintily and lightly tessellated.

lated than the head and thorax, with the sculpturing usually especially light to absent on the excavated apical one-third of the exterior face of the hind tibiae (fig. 55D). The legs blackish to dark brownish, with cream-colored to whitish maculations that, in the case of the fore and middle tibiae, tend to extend about halfway down the exterior face of the joint and, in the case of the hind tibiae, along the posterior margin of the joint for a distance greater than half the length of the joint (but these maculations, sometimes of more limited extent and in a specimen from Itaituba, Brazil, and in another from Faro, Brazil, almost lacking). The apical tarsal joint ferruginous and the other tarsal joints more or less so. A pale sericeous sheen over most of the joints (with the exception of much of the outer face of the hind tibiae) due to very microscopic appressed hairs, but erect hairs few. Such erect hairs are silvery gray and are present on the coxae (particularly the hind pair anteriorly); the trochanters beneath; inconspicuous on the under side of the fore tibiae; a little more abundant and longer on the under side of the middle tibiae; along the lower one-half of the anterior lateral contour of the hind tibiae as well as along the posterior lateral contour of the joint, but the hairs tend to be a little longer on the anterior lateral contour; a few much longer hairs on the outer face of the hind tibiae; along the posterior lateral contour of the metatarsi but short. The metatarsal brushes tend to be light golden to reddish golden.

WINGS: Almost clear and transparent, iridescent. The venation and stigma brownish to blackish, with at least the upper half of the first transverse cubital vein and the entire second transverse cubital vein usually rather clearly demarked. The tegulae dark reddish to brownish black with almost invariably a cream-colored maculation anteriorly; the root of the wing usually immaculate, rarely (a specimen from Ivon, Río Beni, Bolivia, and one from Teffé, Brazil) with a pale spot. The number of hamuli per lower wing is usually five, more rarely six. Of 30 wings examined, 26 had five hamuli and four had six hamuli, an average of 5.13.

ABDOMEN: Black to dark reddish black. When telescoped, which is usually the case,

the tergites present a densely and uniformly granular surface devoid of shiny interspaces, hardly distinguishable from the opaque integument of the head and thorax. When the abdomen is extended, however, and the usually concealed bases of the tergites are revealed, these prove to be sculptureless (or nearly so) and polished. The tergites devoid of erect hairs, but with very microscopic appressed pale hairs that produce a sericeous sheen when the light strikes them. The hair of the venter as indicated in the description of the subgenus.

MEASUREMENTS: Length 4.5 mm. (abdomen much telescoped) to 6 mm.; width of thorax 1.75 to 2 mm.; length of forewing, including tegula, 4.25 to 4.75 mm. The minimum measurements apply to specimens from Carvoeira, State of Amazonas, Brazil, and the maximum measurements to specimens from Peru, especially Iquitos.

QUEEN

Unknown.

MALE¹

HEAD: A very little wider than it is long, about in the proportion that 9.75 is to 9, nearly circular in contour, barely if at all narrower than the distance that separates the outer rim of one of the tegulae from the outer rim of the other. The face very narrow. The distance from one eye to the other at their level of closest approximation (below) is a trifle less than one-half the length of the eye, whereas in the worker of *prosopiformis* the shortest distance between the eyes is about three-fourths of the length of the eye. The distance that separates the eyes at their level of closest approximation about as 3.75 is to 4.50 when compared to the distance between them at the level just below the anterior ocellus and about as 3.75 is to 8 when compared to the distance separating the anterior ocellus from the apex of the clypeus. The clypeus about two-thirds as long as its maximum width, small, distinctly arched, six sided, the apex widely truncate along the middle and rather sharply receding to each side, the apico-lateral angles nearly rectangu-

¹ Description based on a male from Restrepo, Colombia

lar and virtually grazing the inner orbits of the eye. The labrum simple. The mandibles rather thumb shaped in outline, short, in contact but not overlapping, wide at the base, narrowed towards the apex, which is edentate and has the inferior margin convex. The malar space surviving only as a small triangle towards the outer angle of the base of the mandible, the inner angle of the base of the mandible being in contact with the rim of the eye. The distance between the lateral ocelli fully twice the major axis of an ocellus; the distance separating each lateral ocellus from the nearest compound eye about equal to the diameter of an ocellus. The region behind the ocelli thickened and raised. The sculpturing of the head, like that of most of the other parts, exceedingly dense and fine, the entire integument of the head dull and opaque owing to a microscopic granular surface (a little suggestive of the striking surface of a matchbox) that is utterly devoid of shiny interspaces. The scape robust; when viewed from the side, emphatically wider than the flagellum; short, barely more than one-fourth the length of the flagellum. The head black, but with the following areas yellow: the scape in front and laterally, being darkened somewhat only posteriorly; a narrow stripe, tapering above and somewhat emarginate at the level of the antennal sockets, that extends along the inner orbit of the eye almost to the level of the anterior ocellus; a solid triangle in the supraclypeal area; the clypeus except for two subparallel brownish black longitudinal stripes in the basal half. The almost wholly black mandibles are red apically, the almost wholly black flagellum is dull reddish below, and the antennal sockets incline to be reddish. The erect hairs very few and silvery gray, being confined to the vertex, the lower one-third of the genal area, apex of mandibles below, and labrum. A sericeous sheen is imparted to the head by the presence of appressed, very microscopic silvery gray hairs on the genal area, front, sides of face, and clypeus.

THORAX: Sculptured like the head, exceedingly densely and finely granular to tessellate, very opaque; only on the propodeum is the sculpturing a little less delicate and less crowded. The width of the meso-

notum at its maximum, near the anterior margin, a little greater than its length (about as 8 is to 7); the combined length of the mesonotum and scutellum compared to the maximum width of the mesonotum about as 10.5 is to 8. The flat scutellum fully three-fifths as long as it is wide, extending backward so far that, when it is viewed from above, it conceals or very nearly conceals the propodeum (much as in *opaca*); the rounded hind margin of the scutellum, in the specimen on which this description is based, with a nick-like emargination at the middle. The tubercles deflected relatively little from the horizontal to the vertical (more nearly orientated like those of *lineata* and *petropolis* than like those of *opaca*) and shaped somewhat like a mussel shell. The thorax almost completely devoid of erect hairs, very short silvery gray hairs being only on the under side (especially laterally) of the scutellum. The mesonotum and mesopleura without erect hairs, and such hairs are sparse and short even on the mesosternum, where the conspecific worker has them in abundance. The mesonotum, scutellum, and especially mesopleura with a sericeous sheen due to their being covered with very microscopic, silvery gray appressed hairs. A dense, rather conspicuous patch of silvery gray to whitish tomentum at each side of the bare dorsal and middle region of the propodeum. The thorax black, with the following areas yellow: a transverse stripe, medianly interrupted, along the posterior margin of the pronotum; the tubercles; a stripe along the lateral margin of the mesonotum to the inclusion of the axillae, to be continued (after an interruption) along the posterior margin of the scutellum.

LEGS: With tessellation far more delicate than that of the other parts of the body. Brownish black, with light yellowish to cream-colored stripes extending the entire or virtually the entire length of the outer face of the tibiae [narrowed along the middle in the case of the stripe on the fore and middle tibiae with a flanking area of black on each side, and bordering the posterior margin (fig. 55H) in the case of the stripe on the hind tibiae]. In addition, there is a pale yellow to cream-colored stripe on the outer face of the fore metatarsi; the middle and hind metatarsi and the small joints of the tarsi are red. The

legs almost devoid of erect hairs. There are a few such silvery gray hairs on the hind coxae but they are very short. The silvery gray tomentum on the middle and hind trochanters is almost microscopic as is the fringe of minute whitish hairs near the base of the under side of the fore femora. A few hairs on the under side of the fore tibiae, somewhat longer hairs on the under side of the middle tibiae, and a few anteriorly at the apex of the hind tibiae, all silvery gray. The hairs externally on the metatarsi few, very short, and inconspicuous, confined largely to the sides, especially posteriorly. The hairs on the inner face of the metatarsi golden to reddish golden. In addition to the negligibly few erect hairs there is visible under illumination a sericeous sheen, due to the presence of very microscopic silvery gray appressed hairs.

WINGS: Almost clear and transparent, iridescent. The venation and stigma brownish black, with at least the upper one-half of the first transverse cubital vein and the entire second transverse cubital vein rather clearly demarked. The tegulae brownish to somewhat blackish with a cream-colored to yellowish maculation anteriorly. The number of hamuli five on each lower wing.

ABDOMEN: Dull black to sometimes dull dark reddish black. When telescoped, the tergites present a densely and uniformly granular surface devoid of shiny interspaces and hardly to be differentiated from the opaque integument of the head and thorax. But when the abdomen is extended, revealing the usually concealed basal half of each tergite, this basal half proves to be much more lightly tessellated. The tergites devoid of erect hairs except for a fringe of moderately long, pale, incurved hairs along the apex of tergite 7, but with a sericeous sheen, when viewed from certain angles, that is due to very microscopic, appressed, silvery gray hairs. The sternites more strongly silvery gray sericeous but also largely devoid of erect hairs. Sternite 4 somewhat depressed medianly and with a very small semicircular emargination medianly at the apex that is flanked on each side by a subtubercle-like, slightly in-pointing protrusion of generally rounded contour that is fringed with short hairs. Sternite 5 likewise depressed medianly but with a very wide and very deep semicircular emargination that

penetrates almost to the very base of the sternite where only a thin membranous connection survives. The sundered (or nearly sundered) lateral lobes resulting on each side of the median emargination are each armed at the inner end of their apex with a club-shaped, partly hair-fringed protrusion that slants inward and downward towards its fellow for a distance greater than that which separates the two protrusions at their apices. The median spine of sternite 6 wide and short; the lateral "shoulders" of this sternite outlined by a thickening of the chitin but their tips united with the median spine by a thinner connecting layer of chitin. (Fig. 63.)

MEASUREMENTS: Length about 6 mm.; width of thorax about 2 mm.; length of forewing, including tegula, about 4.75 to 5 mm.

TYPE MATERIAL

The species *prosopiformis* was erected by Gribodo on the basis of a single worker from Pévas, Peru. According to Horn (1926) the Hymenoptera of Gribodo (and presumably among them the type of *prosopiformis*) were acquired by the museum in Genoa.

DISCUSSION

The notably thickened scape of *prosopiformis* and its more robust stature separate *prosopiformis* from its near relatives of black basic color. *Trigona* (*Paratrigona*) *haeckeli*, like *prosopiformis*, has the scape much thickened, but the prevailing fulvous coloration of *haeckeli* and its smaller size (not to mention other distinctions) make confusion with *prosopiformis* impossible. In respect to its long scutellum *prosopiformis* is closely affiliated with *opaca*, but structurally it stands apart from that species through its stout scape (notably narrow in *opaca*), the parallel rather than apically convergent arrangement of the eyes of its worker, and its less vertically placed tubercles. Comparison of the abdominal sternites of the male of *prosopiformis* (fig. 63) with the corresponding sternites of the male of *opaca* (fig. 58) offers further evidence of the structural differences separating the two species.

One of the footnotes attached to the description of the worker of *prosopiformis* here offered calls attention to the fact that in several instances the quadridentate character

of the mandible of *prosopiformis* has been misinterpreted. This misinterpretation is doubtless owing to the fact that sometimes a connecting septum of chitin obliterates the distinctness of the dentition in the case of the two outermost teeth, and that the two innermost teeth may have escaped observation

it is the specimens from Peru and from Bolivia that have the longer maculations on the legs, those from Brazil having more limited maculations. But the distinction is not absolute, and specimens from Teffé and from Carvoeira, both in the State of Amazonas, have, on the legs, stripes as fully developed as those

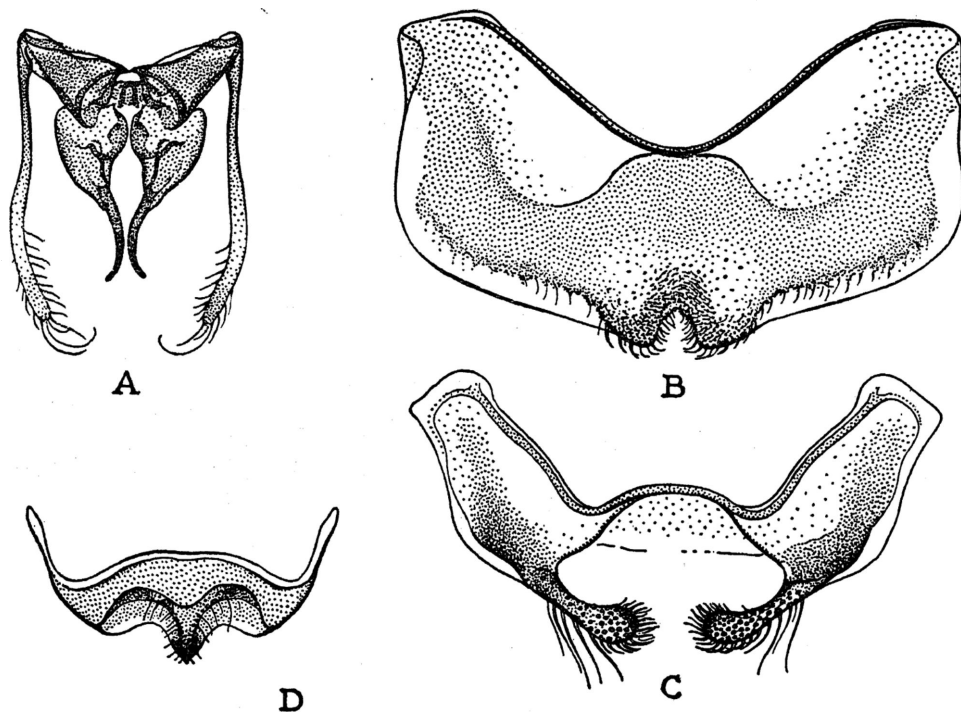


FIG. 63. Abdominal parts of male of *Trigona* (*Paratrigona*) *prosopiformis* (Gribodo). A. Genitalia (chitinized parts only). B. Sternite 4. C. Sternite 5. D. Sternite 6. All based on a specimen from Restrepo, Department of Meta, Colombia. Drawings by Shirley H. Risser.

because of their frequent partial concealment under the labrum.

Friese's *longicollis* has usually been made a synonym of *prosopiformis*, but perhaps it should be considered, instead, a variety of that species, differentiated by the very abbreviated to absent maculations on the outer face of the hind tibiae. Friese in his description (1903, pp. 360-361) omits mention of maculations on the legs of *longicollis*, and a specimen from Itaituba, the type locality, which was identified by Friese as *longicollis* and which I have seen, belongs distinctly to the group of limited maculation. In general

in specimens from the west coast of South America.

There is no information available regarding the nest or nest habits of *prosopiformis*.

DISTRIBUTION

Gribodo described *prosopiformis* from Pévas, Peru. Friese's *longicollis* [a synonym (?) of *prosopiformis*] was from Itaituba in the Brazilian State of Pará. Ducke added to the recorded distribution of *prosopiformis* localities in the State of Amazonas, eastern Peru, and southeastern Colombia. Among the specimens before me some [those from Teffé in

Amazonas, July, 1906 (A. Ducke), and those from Iquitos in Peru, May 2, 1920 (H. Parish), and August 1, 1920 (Cornell University Expedition)] duplicate localities already cited by Ducke, but others extend the range to the inclusion of Bolivia, as follows:

PERU: Iquitos (H. Bassler), May 2, 1920 (H. Parish), and Aug. 1, 1920 (Cornell Univ. Exped.); Puerto Bermudez, Río Pichis, July 12-19, 1920 (Cornell Univ. Exped.)

BOLIVIA: Riberalta, Río Beni, Jan. (W. M. Mann); Ivon, Río Beni, Feb. (W. M. Mann); Rurrenabaque, Río Beni, Dec. (W. M. Mann).

BRAZIL: State of Amazonas: Carvoeira, Aug. 26, 1924 (J. Bequaert); Faro, Dec., 1905. State of Matto Grosso: Corumbá.

COLOMBIA: Department of Meta: Restrepo, 500 meters, 1936, male (J. Bequaert).

Trigona (*Paratrigona*) *haeckeli* Friese

Trigona haeckeli FRIESE, 1900a, p. 393.

Melipona haeckeli, DUCKE, 1916, opposite p. 28, p. 106.

Melipona haeckeli, DUCKE, 1925, pp. 343, 352, 401.

Trigona (*Paratrigona*) *haeckeli*, SCHWARZ, 1938, p. 496, pl. 58, figs. E, E'.

Paratrigona haeckeli, MOURE, 1944a, p. 71.

Melipona haeckeli, DUCKE, 1945, opposite p. 24, p. 81.

WORKER

DIAGNOSTIC CHARACTERS: Bright fulvous with ill-defined pale maculations. Scape notably swollen, at its widest (about the middle) approximately twice the width of the flagellum, which is darker than the rest of the head. The flagellum short, with the intermediate joints distinctly wider than long. The pale maculations of the head diffuse, so that the fulvous parts are reduced to small areas of survival, the most conspicuous patches of fulvous being often two large twin ovals on the front. Scutellum about two-thirds as long as it is wide. The maculated tubercles deflected only a little from the horizontal. A fairly wide stripe rimming the sides of the mesonotum to the inclusion of the axillae and continuing, somewhat narrowed, around the posterior rim of the scutellum. An irregular, somewhat W-shaped maculation on the upper and anterior half of mesopleura. Abdomen, when telescoped, presents a rather uniformly, if lightly, tessellated surface viewed from above.

HEAD (FIG. 62E): A little wider than long, about in the proportion of 8 to 7, its width somewhat greater than the distance from the outer rim of one of the tegulae to the outer rim of the other tegula. The face narrow, the distance between the compound eyes at a level just below the middle ocellus being about two-thirds that from the anterior ocellus to the apex of the clypeus. The compound eyes barely convergent below, the distance separating them below being almost the same as that which separates them near their summit. The clypeus about one-half as long as it is wide, very slightly arched, six sided, the apex widely truncate along its middle, more briefly but rather distinctly receding at each side of apical middle, the apico-lateral extremities distinctly less than rectangular and separated from the nearest compound eye by rather less than one-half the width of the flagellum. The supraclypeus small but rather prominent. The labrum slightly and rather evenly thickened, simple. The mandibles (fig. 62E1) overlapping each other, wider at their base and at their apex than they are at the middle; quadridentate along the apex, the second tooth (counting from the outermost inward) being the widest and bluntest, but the two outer teeth sometimes not so clearly defined as the two innermost owing to a thin connecting septum of chitin between these outer teeth that tends to obliterate their outline. The malar space subtriangular, large on its outer one-half or more but distinctly shortened inward, with the inner angle of the base of the mandible almost in contact with the rim of the eye. The labrum rather evenly thickened, simple. The distance between the lateral ocelli (about twice the major axis of an ocellus) somewhat greater than that which separates each lateral ocellus from the nearest compound eye. The vertex slightly thickened and raised behind the ocelli. The sculpturing of the head exceedingly dense and fine, the entire head, viewed from in front, being dull and opaque owing to a microscopic granular surface (a little suggestive of the striking surface of a matchbox) that is utterly devoid of shiny interspaces. The sculpturing somewhat finer on the genal area, especially the inferior one-third of this area, which is sometimes faintly shiny. The scape notably swollen. Relatively slender at the

base, it is much expanded towards the middle, its inner contour being strongly convex. At its widest it is about twice the width of the flagellum, and its length is about half that of the flagellum. The head, like the rest of the body, bright fulvous, but with diffuse pale maculations reducing the areas of fulvous for the most part to mere patches. The pale areas are: almost the entire scape, which is darkened only posteriorly, especially towards the apex; a conspicuous stripe of very irregular width along the entire inner orbit of the eye (this stripe is knob-like below, where it makes contact with the side of the clypeus, has a bulging convex expansion at its middle, and at its upper extremity unites with a stripe that zigzags behind the ocelli and the continuation of which, much narrowed, may be traced along the entire posterior orbit of the eye); from the middle ocellus downward extends a narrow stripe that halfway from the supraclypeus expands rather abruptly, becoming more or less coalescent sometimes with the convex expansion (above referred to) of the stripe that borders the anterior orbit of the eye; the entire clypeus except for its brownish hyaline bounding lines, all of which are narrow, the least narrow being that along the apex; a solid equilateral or almost equilateral triangle in the supraclypeal area; the labrum; the mandibles except for their brownish hyaline basal prominences and their brownish to blackish apex, including the teeth. In contrast to the scape the flagellum is black both above and usually below, but the several joints of the flagellum viewed from the under side tend to reveal an exceedingly narrow pale ring at their apex. The head is almost completely devoid of erect hairs, these consisting of a few silvery gray hairs on the lower one-third of the cheeks, a few yellowish hairs fringing the lower edge of the mandibles, and a few stunted pale hairs on the labrum; the vertex is devoid of erect hairs. The head is covered in large part by very microscopic, silvery gray, appressed hairs, not readily visible unless the light strikes them, when they impart a faint sericeous sheen to the otherwise dull integument.

THORAX: With granular sculpturing as fine, dense, and dull as that of the head; the sculpturing on the propodeum a little less delicate and a little less crowded than that of

the other parts. The width of the mesonotum at its greatest, near the anterior rim, when compared to its length, is about as 6 is to 5, but the combined length of the mesonotum and scutellum when compared to the maximum width of the mesonotum is about as 7.75 is to 6. The very flat scutellum is fully two-thirds as long as it is wide, extending backward so far that, when it is viewed from above, it conceals the propodeum (its backward extension seems to be somewhat greater than is the case in *opaca* and *prosopiformis* and the posterior contour of the scutellum is a half oval rather than hemispherical). The tubercles deflected only slightly from the horizontal, a little resembling a mussel shell in shape. The thorax in dorsal view utterly without erect hairs, as are also its sides. Only on the mesosternum are there fairly long and dense silvery gray to slightly yellowish hairs. There is a sericeous sheen due to exceedingly microscopic silvery gray hairs that is traceable, under favorable illumination, especially on the mesopleura. The thorax is, like the head, predominantly bright fulvous but the mesonotum is usually speckled over, leopard-like, with darker spots, and the following areas are pale yellow to cream-colored: a transverse stripe (rarely interrupted medianly) on the posterior half of the pronotum and preceded by a much narrower transverse stripe on the anterior margin; the tubercles (broadly below, briefly stripe-like towards their upper and inner carinated extremity); a fairly wide stripe rimming the side of the mesonotum to the inclusion of the axillae and continuing, somewhat narrowed, around the posterior rim of the scutellum; an irregular, somewhat W-shaped maculation on the upper and anterior half of the mesopleuron; the entire upper plate of the metapleuron (the plate immediately below the hind wing); a small maculation (easily overlooked) at the edge of, and more or less concealed by, the silvery gray to whitish tomentose area that lies at each side of the bare middle area of the propodeum.

LEGS: More delicately and faintly tessellated than the head and thorax, with the sculpturing especially light to absent on the excavated apical one-third or more of the exterior face of the hind tibiae (fig. 55G). The legs fulvous, with very faint and much

diluted markings, barely traceable on the basal half of the external face of the fore and middle tibiae as a faint, almost extinguished, pale stripe that nevertheless suggests the maculation present in *opaca* and *prosopiformis*, and the vestige of a stripe along the posterior margin of the hind tibiae, again suggestive of the condition in these two species. The legs have a pale sericeous sheen over most of the joints (with the exception of much of the outer face of the hind tibiae) due to the presence of very microscopic, silvery gray, appressed hairs, but the erect hairs are few. Such erect hairs are silvery gray and are present on the coxae (especially the anterior face of the hind coxae); the trochanters beneath (rather dense on the middle pair and fairly long on the hind pair); inconspicuous on the under side of the fore tibiae; a little more in evidence and somewhat longer on the under side of the middle tibiae; along the lower one-half of the anterior lateral contour of the hind tibiae as well as along the posterior lateral contour of this joint, the hairs along the anterior lateral contour being usually about as long as, to a trifle longer than, those along the posterior lateral contour. A few much longer hairs on the outer face of the hind tibiae. A moderately long fringe bordering the posterior lateral contour of the fore and middle metatarsi. The metatarsal brushes tend to be light golden.

WINGS: Rather evenly clear¹ and transparent, iridescent. The venation and stigma ferruginous to light brownish; the first and second transverse cubital veins rather feebly indicated. The tegulae fulvous, with a light yellow to cream-colored maculation anteriorly and the root of the wing sometimes with a maculation of like coloration. The number of hamuli, in the six lower wings available for examination, uniformly five.

ABDOMEN: Wide, distinctly wider than the mesonotum, about coextensive with the outer rims of the tegulae. When telescoped, it presents a rather uniformly tessellated surface, but the tessellation is much less dense and opaque than the sculpture on the head and thorax, the dorsal surface of the abdomen being semi-shiny. When the ab-

domen is extended, the usually concealed bases of the tergites prove to be sculptureless and polished. The tergites devoid of erect hairs; covered, however, with very microscopic, appressed, silvery gray to yellowish hairs that impart a sericeous sheen to the surface when the light strikes them. The hair of the venter as described for the subgenus. Abdomen bright fulvous like the other parts.

MEASUREMENTS: Length 3.5 to 4 mm.; width of thorax 1.25 to 1.5 mm.; length of forewing, including tegula, about 3.75 mm.

QUEEN

Unknown.

MALE

Unknown.

TYPE MATERIAL

The species was described from Callanga, Peru. The depository of the type material is not indicated. Three metatypes are in the American Museum of Natural History.

DISCUSSION

Friese's description (1900a, p. 393) of *haeckeli* is very brief. He did not indicate the extent of the pale maculations. Ducke (1916, p. 106; 1925, p. 401; 1945, p. 81) merely stated that the maculations of *haeckeli* are the same as those of *prosopiformis* and *lineata*, but more subdued. However, strictly speaking, *prosopiformis* and *lineata* do not fully conform with each other in their maculations, although in many respects their ornamentation is identical. The maculations cited in the present description are those that characterize three specimens (the only ones available to me) collected by Ducke at Itaituba, which is one of the very few localities from which *haeckeli* is known. These specimens bear name labels in Friese's handwriting, and two of them, in addition, have Friese's metatype label. If the specimens are representative in respect to their maculations, then *haeckeli* resembles *opaca* variety *ornaticeps* (fig. 54D) rather more closely in respect to its facial and thoracic maculations than it does either *prosopiformis* or *lineata*.

Trigona haeckeli shares with *prosopiformis* the swollen scape that especially differentiates that insect from several of its near

¹ According to Friese's original description the apex is more obscure, but this condition is barely traceable in the Itaituba specimens, the only ones before me.

relatives and it is, as Ducke has pointed out (1916, p. 106; 1925, p. 401; 1945, p. 81), much like *prosopiformis* in certain other structural respects, although readily differentiated by its much smaller size and very different coloration. In respect to its color *haeckeli* illustrates about the same degree of isolation from its darker-colored relatives as does the fulvous *atomaria* with respect to *duckei* and the other minute *Trigona* of the subgenus *Hypotrigona*. So exceptional indeed is *haeckeli* in coloration when compared with its closest relatives that it is possible (although far from likely) that it is the callow form of some dark-colored species. In rejection of this interpretation, it will be recalled that *haeckeli* was erected by Friese on the basis of only two specimens, presumably taken in the open, and that the specimens subsequently reported by Ducke from Itaituba were probably collected in the field and not from a nest, for Ducke stated that the nest is unknown. The insect is apparently a very rare one. Nothing is known of its biology.

DISTRIBUTION

As yet recorded only from Callanga, Peru, from Río Tapajoz, and Itaituba in the Brazilian State of Pará. The specimens before me are all from the last-mentioned locality.

Trigona (Paratrigona) impunctata (Ducke)

Melipona punctata, DUCKE, 1901, p. 65.

Melipona punctata, DUCKE, 1902a, p. 419.

Melipona (Trigona) punctata, DUCKE, 1902b, pp. 293, 323-324.

Trigona punctata, FRIESE, 1903, p. 361.

Trigona punctata, MARIANNO, 1911, pp. 122-123.

Melipona impunctata DUCKE, 1916, opposite p. 28, pp. 33, 101-103.

Melipona impunctata, DUCKE, 1925, pp. 343, 352, 398-399.

Melipona impunctata, ALFKEN, 1930b, p. 9.

Trigona (Paratrigona) impunctata, SCHWARZ, 1938, pp. 447, 488-489, pl. 58, figs. A, C, C', pl. 62.

Trigona (Paratrigona) impunctata, SCHWARZ, 1940, p. 9.

Paratrigona impunctata, MOURE, 1944a, p. 71.

Melipona impunctata, DUCKE, 1945, opposite p. 24, pp. 25, 78.

WORKER

DIAGNOSTIC CHARACTERS: Black, with maculations. The scape slender, no wider than the flagellum, the intermediate joints of which are about as long as wide. A stripe on the scape in front; a very narrow stripe along the inner orbit of the eye up to nearly the level of the middle ocellus; a transverse stripe parallel with and close to the apical truncation of clypeus (stripe sometimes interrupted at the middle); a triangular figure on the supraclypeus. Front with numerous erect hairs. Scutellum three-fifths as long as wide. Tubercles almost horizontal in position. A narrow, somewhat discontinuous stripe along the sides of the mesonotum, over the axillae (where the stripe is usually somewhat widened), and around the posterior rim of the scutellum, the interruptions in the continuity occurring immediately before and also behind the axillae. Thorax relatively hairy. Tergites 1 and 2 largely smooth and polished; the tessellation along the apex of the subsequent tergites, the only part with sculpturing, very feeble compared with the granular appearance of the head and thorax. These tessellated apical areas of the abdominal tergites with numerous hairs.

HEAD (FIG. 62, A AND C): Rather large, wider than long, in the proportion of about 10 to 8.5, and just about as wide as the distance separating the outer rim of one of the tegulae from the outer rim of the other. The facial quadrangle a little less narrow than in any other known *Paratrigona* except *isoptero-phila*, the distance between the compound eyes at a level just below the anterior ocellus being more nearly three-quarters than two-thirds the distance from the anterior ocellus to the apex of the clypeus. The compound eyes rather distinctly convergent below, the distance separating them at their level of closest approximation about as 4.75 is to 5.5 when compared to their divergence at the level just below the anterior ocellus. The clypeus a trifle more than one-half as long as its greatest width, gently arched, a little more elevated than the sides of the face, six sided, the apex rather widely truncate along the middle, somewhat less extensively receding to each side, the lateral boundaries almost parallel at the base but strongly divergent towards the apex, the apico-lateral extremi-

ties distinctly less than rectangular but not strongly acute and distinctly separated from the nearest compound eye. The supraclypeus about as prominent as the clypeus. The labrum slightly thickened. The mandibles (fig. 62C1) overlapping each other, wider at their base and their apex than they are at the middle; with four¹ teeth along their apex, the second tooth (counting from the outside inward) nearly as acute as the other teeth, not notably blunt or subtruncate as in most *Paratrigona*, but frequently joined to the first tooth by a septum of chitin. The malar space subtriangular, notably longer at its outer extremity than the width of the flagellum but narrowed to about one-half the width of the flagellum at its inner extremity. The labrum simple. The distance between the lateral ocelli (about twice the major axis of an ocellus) a little greater than that which separates each lateral ocellus from the nearest compound eye. The vertex somewhat carinate behind the ocelli. The sculpturing of the head viewed from in front densely and finely granular, especially over the front, with resulting opacity, the clypeus and adjacent part of the sides of the face with a little less crowded and more delicate sculpturing, faintly shiny, and the sculpturing still finer on the upper two-thirds of the genal area, the lower extremity tending to be sculptureless and polished. The scape slender, no wider than the flagellum and about one-half its length. The head black, with the following light yellow maculations: a stripe, usually clearly defined, from base to apex along the scape in front; a very narrow stripe of rather uniform width extending along the inner orbit of the eye from a level a little below the anterior ocellus downward for the full extent of that inner orbit; a transverse stripe parallel with and close to the apical truncation of the clypeus, its extremities almost in contact with the lower terminus of the stripes bordering the inner orbits of the eye [frequently

¹ Ducke in describing *impunctata* (1916, pp. 101-103) stated that it had a tridentate mandible, doubtless having before him a specimen presenting the not uncommon condition of a partial fusion of denticle 1 with denticle 2 due to an intervening septum of chitin. Even in such cases, however, the two denticles are very clearly traceable as individuals, while in numerous other cases where the septum is absent the mandible is unmistakably quadridentate.

this stripe is obscured or interrupted at the middle, only its extremities surviving² (fig. 62C)]; a solid triangle on supraclypeus, often a little emarginate with black on its lowest side but only very exceptionally reduced to a mere up-pointing angle as is the case in the corresponding maculation in *opaca* variety *opaca*; exceptionally (specimens from the upper Essequibo River) with a short narrow stripe at the lower extremity of the outer orbit of the eye. The mandibles, usually ferruginous except for the basal prominences and the teeth, may sometimes be largely black on their basal half (specimens from Waratuka and Amatuka); the labrum ferruginous, sometimes more or less sooty, and the flagellum as a rule more or less ferruginous beneath. In contrast to the glabrous condition of the front in the known *Paratrigona* other than *isopterophila*, the present species has numerous erect, moderately long, silvery gray to yellowish (in some instances even brown) hairs in this area in addition to the microscopic appressed hairs that are dense over the entire head viewed from in front to the inclusion of the clypeus. The clypeus itself without or with only exceedingly microscopic erect hairs, but on the lower part of the genal area, on the inferior margin of the mandibles, on the labrum, and on the vertex such erect hairs, all silvery gray, occur. There are in some specimens even a few very short silvery gray hairs on the scape.

THORAX: About as densely granular and lusterless as the front of the head; only on the propodeum is the sculpturing a little coarser and less crowded. The thorax relatively short; the width of the mesonotum at its maximum, near the anterior margin, about as 7.5 is to 5.5 when compared to its length but the combined length of the mesonotum plus the scutellum is about as 8.5 is to 7.5 when compared with the maximum width of the mesonotum. The rather flat scutellum about three-fifths as long as it is wide, its posterior rim, sometimes faintly emarginate at the middle, is widely hemispherical, extending backward so as to conceal or nearly conceal the propodeum when the insect is viewed from above. The tubercles almost horizontal in po-

² Especially does this condition apply to most of the specimens from British Guiana.

sition. The erect hairs far more numerous and longer than in the known *Paratrigona* other than *isopterophila*. There are silvery gray erect hairs on the mesopleura, mesonotum, dorsal surface and posterior rim of the scutellum (rarely with a few darker hairs intermixed), and on the mesosternum, the hairs of the scutellum and of the mesosternum being conspicuously longer than those of the other areas. In addition, the mesopleura and mesonotum and scutellum are silvery gray tomentose, the mesopleura almost as densely so as the metapleura and the area at each side of the bare middle region of the propodeum. The thorax black with the following areas pale yellow: a transverse stripe (sometimes interrupted medianly) over the posterior half of the pronotum supplemented as a rule by a narrower transverse band along the anterior margin of the pronotum; the tubercles; a narrow, somewhat discontinuous stripe along the lateral margin of the mesonotum, over the axillae (where the stripe is somewhat widened as a rule), and around the posterior rim of the scutellum, the interruptions in this stripe occurring both immediately before and behind the axillae.

LEGS: More robust than in *lineata*, *petropolis*, or *opaca* and less extensively tessellated. The front and middle tibiae very finely and rather densely tessellated on their outer face; the posterior tibiae densely tessellated over their inner face, and the posterior face of the femora is also lightly and thinly tessellate; but the anterior face of the fore and middle femora is polished and shiny as is the outer face of the hind tibiae. The legs black or sometimes brownish and at least the apical tarsal joint tends to be ferruginous, but as a rule there are no pale maculations (only in rare cases can a tiny pale spot be traced at the base of the tibiae¹). The hairs more abundant than in *Paratrigona* other than *isopterophila*. There are silvery gray hairs on the coxae (especially long on the hind coxae anteriorly), on all the trochanters beneath (very dense on the middle trochanters and rather long on the hind trochanters), on the under side of the front and middle

femora, and to a less extent on the upper side usually of at least the hind femora near the apex. The present species has short, erect, silvery gray hairs even on the outer face of the fore and middle tibiae (a condition unusual in *Paratrigona*), but these hairs are shorter than the coarser and sometimes darker hairs that fringe the lateral contours of these tibiae and shorter, too, than the silvery gray or sometimes darker hairs on the under side of at least the middle tibiae. In addition, the front and middle tibiae have on their outer face a covering of appressed, microscopic, silvery gray hairs. The hind tibiae fringed along their anterior and posterior lateral contours with rather long hairs, those along the anterior contour being sparser but a little the longer; in color these hairs range from silvery gray to blackish, those along the posterior contour being often darker than those of the anterior contour; a few still longer hairs on the outer face of the hind tibiae. On the outer face of the front and middle metatarsi there are erect, usually silvery gray hairs and there is also a fringe of such hairs along the posterior lateral contour of these metatarsi; the external face of the hind metatarsi with rather fewer hairs and these inclined to be dark. The metatarsal brushes tend to be copper colored.

WINGS: Almost clear and transparent, iridescent. The venation and stigma brownish, with the first transverse cubital vein rather clearly demarked, the second transverse cubital vein a little fainter but nevertheless traceable without difficulty. The tegulae dark reddish brown, sometimes with a small yellow spot anteriorly (Prata and "near Pará," Brazil) but no maculation at the root of the wing. The number of hamuli per lower wing usually five. Of 57 wings examined, 56 had five hamuli and one had four hamuli, an average of 4.98.

ABDOMEN: Black to very dark reddish black. The basal part of the tergites, when revealed, sometimes, especially in callow specimens, a light brown even when the apical part is black. Tergites 1 and 2 (in contrast to *Paratrigona* other than *isopterophila*) largely smooth and polished, shiny, with very feeble tessellation (largely absent from tergite 1) only along their apical one-third. The apex (usually the only part visible) of the subse-

¹ This maculation characterizes some of the specimens from Vista Alegre in the Brazilian State of Amazonas, and is also traceable in some of the specimens from the upper Essequibo River in British Guiana.

quent tergites with scarcely stronger tessellation, decidedly feeble when contrasted with the dense, granular sculpturing on the head and thorax, but approximating that on the outer face of the fore and middle tibiae. The basal part of these tergites, when revealed, smooth and polished. The tessellated apices of tergites 3 to 6, and to a lesser extent of tergite 2, covered with a hirsute band of semi-erect to appressed hairs; these hair bands silvery gray but sometimes with darker hairs (particularly erect hairs) interspersed. The hairs of the venter as described for the subgenus.

MEASUREMENTS: Length 4.25 to 5 mm.; width of thorax about 2 mm.; length of forewing, including tegula, about 4.25 to 4.5 mm.

QUEEN

Unknown.

MALE

HEAD: Wider than long, in the proportion of about 9.5 to 8, and just about as wide as the distance separating the outer rim of one of the tegulae from the outer rim of the other. The face very narrow. The distance from one eye to the other at their level of closest approximation (below) is about one-half of the length of the eye, whereas in the conspecific worker the shortest distance between the eyes is about five-sevenths the length of the eye. The distance that separates the eyes at their level of closest approximation about as 3.5 is to 5 when compared with the distance between them at the level just below the anterior ocellus, and about as 3.5 is to 7 when compared with the distance separating the anterior ocellus from the apex of the clypeus. The clypeus fully two-thirds as long as it is wide, rather distinctly arched, six sided, the apex widely truncate along the middle and somewhat sharply receding to each side, the apico-lateral angles not far from rectangular and virtually grazing the inner orbit of the eyes. The labrum simple. The mandibles somewhat thumb shaped in outline, rather wide at the base, running to a blunt point at the edentate apex, rather short, their tips meeting (not overlapping), the inferior margin convex in outline towards the apex. The malar space represented by a minute, vestig-

ial subtriangle below the outer half of the apex of the eye, the inner extremity of the base of the mandible being in contact with the rim of the eye. The distance between the lateral ocelli about twice the major axis of an ocellus, and the distance between each lateral ocellus and the nearest compound eye about the diameter of an ocellus. The region behind the ocelli somewhat raised. The sculpturing of the head, viewed from in front, densely and finely granular, especially over the front, with resulting opacity; the clypeus and adjacent part of the sides of the face with a little less crowded and somewhat more delicate sculpturing; and the sculpturing still finer on the genal area, tending to be especially light on the lower one-third of this area. The scape viewed from the side only a little wider than the flagellum and approximately one-fourth as long as the flagellum. The head black but with the following areas light yellow: the entire scape except posteriorly; a narrow stripe, somewhat widened below, extending downward along the inner orbit of the eye from a little below the level of the middle ocellus; a transverse stripe fairly near to, and parallel with, the apex of the clypeus but sometimes medianly dulled or obliterated. Reddish are the apical tip of the mandibles, the antennal sockets, and the flagellum below. The hairs rather more numerous than in other known males of *Paratrigona* with the exception of *isopterophila*. In contrast to the glabrous condition of the front in most males of this subgenus, *impunctata* has numerous semi-erect silvery gray to sometimes brownish hairs in this region in addition to the silvery gray appressed hairs that are present over the head viewed from in front to the inclusion of the clypeus, and also over most of the genal area. The erect hairs on the vertex dark, those fringing the mandibles below and on the lower part of the genal area silvery gray.

THORAX: About as densely granular and lusterless as the front of the head; only on the propodeum is the sculpturing a little coarser and less crowded. The width of the mesonotum at its maximum, near the anterior margin, about as 7 is to 6 when compared to the length of the mesonotum, and about as 7 is to 9 when compared to the combined length of the mesonotum and

scutellum. The rather flat scutellum about three-fifths as long as it is wide; its posterior rim, sometimes with an ultra-feeble emargination at the middle, is widely hemispherical, extending backward so as to conceal or nearly conceal the propodeum when the insect is viewed from above. The tubercles almost horizontal in position. The hairs more conspicuous than in other *Paratrígona* excepting specimens of *lineata* from Lassance, Brazil, and *isopterophila*; only very short and appressed to barely semi-erect over the mesonotum; still very short but erect and silvery gray on the mesopleura; long and dark on the scutellum (particularly along its posterior margin); long and silvery gray on the mesosternum. The propodeum bare on the large dorsal and middle area but flanked on each side by a dense conspicuous area of silvery gray to whitish tomentum. The thorax black but with the following areas light yellow: a transverse stripe (sometimes medianly interrupted) over the posterior half of the pronotum, but in the limited number of specimens before me no supplementary narrower transverse stripe (such as is present in the conspecific worker) along the anterior margin of the pronotum; the tubercles (or wholly black); a short stripe along the lateral borders of the mesonotum, sometimes only coëxtensive with the tegulae or slightly overlapping them; the axillae; a very brief stripe along the posterior margin of the scutellum, widely sundered from the maculation on the axillae.

LEGS: With tessellation far more delicate than that of at least the head and thorax. The anterior face of the fore and middle femora polished, hairless, and shiny. The legs blackish to brownish, with the apical joint of the tarsi usually touched with red but no maculation (contrary to the condition in so many other *Paratrígona*) on the outer face of the tibiae, not even a basal spot. The erect hairs fewer and more stunted than in the conspecific worker, and with the exception of the golden brushes on the inner face of the metatarsi, silvery gray. These silvery gray erect hairs are present on the coxae (especially the hind pair) and on the trochanters (especially the middle trochanters). The femora have a microscopic fringe on their under side, but the outer face of the fore and middle tibiae is

devoid of erect hairs, having only sericeous, appressed, microscopic hairs such as occur also on the posterior face of the several femora, with the addition of a few semi-erect short hairs on the anterior face of the hind femora near the apex. The under side of the fore and especially of the middle tibiae with a few erect hairs. A very few short hairs present on the anterior lateral contour of the hind tibiae (fig. 55I), but even these stunted hairs usually a little less inconspicuous than the feeble evidence of hairs on the posterior lateral contour of these tibiae. Moderately long hairs on the outer face of the fore metatarsi, but the metatarsi of the middle and hind legs with only appressed hairs on their outer face, although there are a few hairs fringing their anterior and particularly their posterior lateral contours.

WINGS: Almost clear and transparent, iridescent. The venation and stigma brownish to blackish, with the first transverse cubital vein rather clearly demarked, the second a little fainter but nevertheless traceable without difficulty. The tegulae dark reddish brown to blackish, with in one of the specimens only (a callow from Kartabo?) a small yellow maculation anteriorly. The number of hamuli, in the six wings examined, uniformly five.

ABDOMEN: Black. Tergites 1 and 2 (in contrast to the usual condition in *Paratrígona*) largely smooth and shiny, tergite 1 wholly or almost wholly so, tergite 2 with the tessellation largely or wholly confined to the apical one-third and very delicate. The apex (usually the only part visible) of the subsequent tergites with scarcely stronger tessellation, decidedly feeble when contrasted with the dense granular sculpturing of the head and thorax, but approximating the sculpturing of the outer face of the tibiae; the basal part of these tergites, when revealed, virtually smooth. The hair bands along the apices of the tergites with the hairs more uniformly appressed than in the worker and hence even somewhat less conspicuous. Tergite 7 fringed with relatively long black hairs. The venter silvery gray tomentose over the apical half of sternites 1 to 5, almost plush-like on the exposed parts of sternites 3 to 5. Sternite 4 is depressed widely over the middle region; its apex, with a

narrow but deep, somewhat rectangular emargination at its middle, is otherwise truncate, the truncation terminating at each of its lateral extremities in a feeble nipple-like prominence; a fringe of hairs from end to end of the apex. Sternite 5 likewise widely depressed over its middle region; its apex with an emargination at the middle that in width and shape much resembles that of sternite

TYPE MATERIAL

Presumably the type material is for the most part in the Museu Paraense, Pará, Brazil. It included specimens from Oyapock, Pará, Marajó Island, Macapá, Almeirim, Faro, and Itaituba, all in the State of Pará; Teffé in the State of Amazonas; the Madeira-Mamoré Railway in the northwestern part of the State of Matto Grosso; Iquitos in eastern

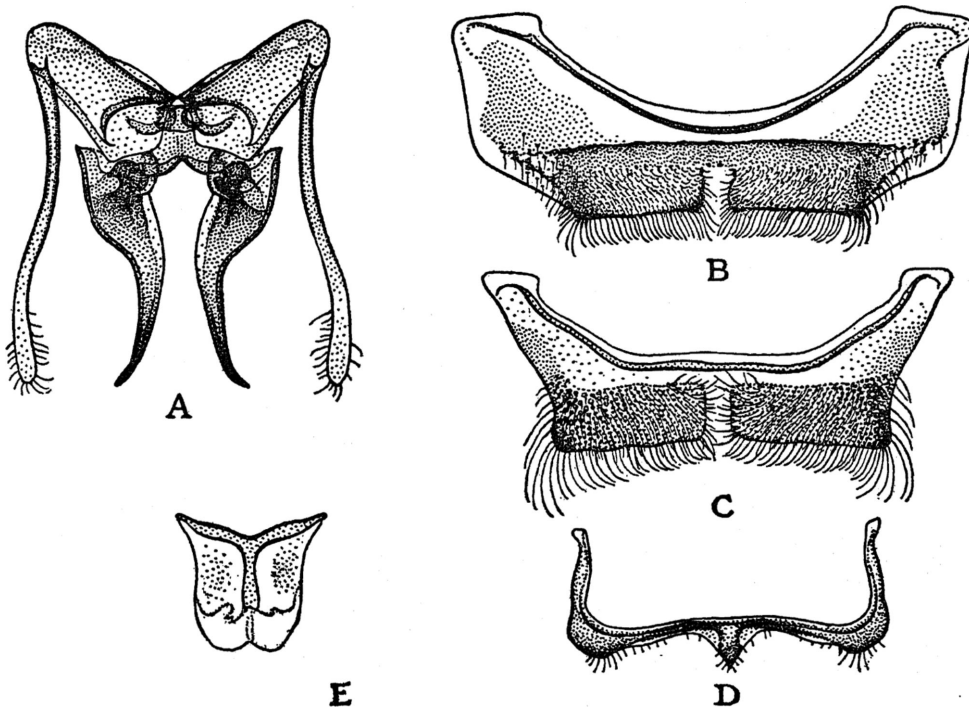


FIG. 64. Abdominal parts of male of *Trigona* (*Paratrigona*) *impunctata* (Ducke). A. Genitalia (chitinized parts only). B. Sternite 4. C. Sternite 5. D. Sternite 6. E. Sternite 7. All based on a specimen from British Guiana. Drawings by Shirley H. Risser.

4, otherwise truncate from end to end and fringed throughout with hairs that are longest at the lateral extremities; these lateral extremities shoulder-like and prominent, being visible even when the bee is viewed from above. Sternite 6 with a short, stout, triangular, median spine the tip of which terminates on approximately the same level as the shoulder-like lateral formations. (Fig. 64.)

MEASUREMENTS: Length 4.5 mm.; width of thorax 1.75 to 2 mm.; length of forewing, including tegula, about 4.5 mm.

Peru. Likewise included in the range, on the authority of Friese, was Bartica, British Guiana.

DISCUSSION

Trigona (*Paratrigona*) *impunctata* (Ducke) is readily separated from its near relatives by characters given in the keys (pp. 353-356). Its specific name (a little misleading in the case of an insect that is distinguished for the density of the sculpture over most of its body) serves to emphasize the most notable respect in which *impunctata* differs from such near relatives as *lineata*, *prosopiformis*, *haeck-*

eli, and *opaca*, namely, the largely smooth and polished condition of the tergites of the abdomen, very similar in the limited sculpturing to the abdomen of *Trigona* (*Nannotrigona*) *testaceicornis* (Lepeletier). In its more robust build, manifested in width rather than in length, it is readily differentiated, too, from all its near relatives except *isoptrophila* and *prosopiformis*. The maculations of the face of *impunctata* when fully developed are rather like those of typical *opaca*, but in *impunctata* the small stripes are lacking that run parallel with, and just outside of, the lateral boundaries of the clypeus of typical *opaca*.

As the description indicates, there is considerable variability in the extent of the maculations and even in the color of the hair among the specimens here grouped under *impunctata*. For the most part specimens from British Guiana are less fully maculated than those here reported upon from Brazil, the stripe along the apex of the clypeus being in the great majority of cases widely interrupted medianly, so that merely two sundered lateral spots survive, and the stripe on the thorax being discontinuous, with a particularly wide gap between the maculations on the axillae and the only partly encircling bordering stripe on the posterior edge of the scutellum. Although these Guianan specimens superficially approximate *isoptrophila*, they have far more in common with *impunctata* and through intergrading specimens seem rather too closely linked to the fully maculated specimens of *impunctata* to justify separation from it as a variety.

A fragment of the nest of this species was included in the vial containing the specimens from Kartabo (A. Emerson). The cells, measuring 2.25 by 4 mm., are arranged compactly and evenly in combs. The nest was obtained, according to Emerson, from a nest of *Nasutitermes* (*N.*) *similis* Emerson, and his field note regarding the *Trigona* nest reads: "Small compartment with smooth interior. Comb in three layers and honey cells under it. All was supported by wax filament structure." Professor Emerson took an excellent picture of the nest, which through his courtesy is here reproduced (pl. 8). It should be stated that the termite nest from which the *Trigona* nest was obtained was a well-

populated one from which Emerson collected "the king, queen, workers and soldiers as well as Staphylinid termitophiles."

There is likewise before me a small series of *impunctata* that Emerson obtained from a nest of *Nasutitermes* (*N.*) *costalis* (Holmgren) on July 31, 1924, at Camaria, British Guiana.

The reader is referred to the discussion of *isoptrophila* (p. 409), which, as the name implies, also establishes itself in termite nests.

Ducke noted (1902a, p. 419; 1916, p. 103; 1925, p. 399; 1945, p. 78) that *impunctata* has an odor resembling that of bedbugs, which may be an aid in field identification for those familiar with the odor of bedbugs.

DISTRIBUTION

Ducke, who described this species, noted that it is spread throughout the Hyläa but is nowhere abundant. He listed (1916, pp. 102-103; 1925, p. 399; 1945, p. 78) localities in the Brazilian States of Pará, Amazonas, and Matto Grosso (northwestern part), as well as eastern Peru and British Guiana (the latter on the authority of Friese).

The British Guianan specimens of Friese were from Bartica. In the collections here reported upon there are specimens from Kartabo, which is in the Bartica District, as well as from several other localities in British Guiana. Most of these specimens are less fully maculated than are the specimens representing localities in the State of Pará and the State of Amazonas.

Specimens here assigned to *impunctata* are from the following localities:

BRAZIL: State of Pará: Pará, Nov. 11, 1900 (A. Ducke); near Pará (H. B. Merrill): Prata, July 9, 1919 (H. Parish). State of Amazonas: Vista Alegre, Rio Branco, Sept. 6, 1924.

BRITISH GUIANA: Kartabo, Oct. 15, 1920, male as well as workers (A. Emerson), June 26, 1922 (W. Beebe); Potaro Landing, Feb. 21, 1921; Camaria, July 31, 1924 (J. F. W. Pearson); Waratuka, May 24, 1929, and Amatuka, with identical date (J. Ogilvie); Waranama, Nov. 16, 1936 (J. Ogilvie).

Trigona (*Paratrigona*) *isoptrophila* Schwarz

Trigona impunctata subspecies *isoptrophila* SCHWARZ, 1934, pp. 6, 21-22.

Trigona (*Paratrigona*) *isoptrophila*, SCHWARZ, 1938, p. 489, pl. 58, fig. B.

WORKER

DIAGNOSTIC CHARACTERS: Black, with limited maculations. Scape moderately robust, at its widest somewhat wider than the flagellum, the intermediate joints of which are about as long as wide. An obscure stripe along the lower one-half to two-thirds of inner orbit of eye, usually a crescentic figure in supraclypeal area, and sometimes a dull spot towards middle of apex of clypeus. Front with erect hairs. Scutellum three-fifths as long as it is wide. Tubercles almost horizontal in position. No evidence of banding laterally on the mesonotum and only faint reddish traces, if any, on axillae and on apical tip of scutellum. Thorax relatively hairy. Tergites 1 and 2 largely smooth and polished; the tessellation along the apex of the subsequent tergites (the only part with sculpturing) very feeble compared with the granular sculpturing of the head and thorax. These tessellated apical areas of the abdominal tergites with numerous hairs.

HEAD (FIG. 62B): Rather large, a little wider than long, in the proportion of about 10 to 8.5, and just about as wide as the distance separating the outer rim of one of the tegulae from the outer rim of the other. The facial quadrangle a little less narrow than in any known *Paratrigona* other than *impunctata*, the distance between the compound eyes at a level just below the middle ocellus being more nearly three-quarters than two-thirds that between the middle ocellus and the apex of the clypeus. The compound eyes rather distinctly convergent below, the distance separating them at their level of closest approximation about as 4.75 is to 5.5 when compared to their divergence at the level just below the middle ocellus. The clypeus barely more than one-half as long as its greatest width, gently arched, a little more elevated than the sides of the face, hexagonal, the apex truncate along the middle, receding to each side, the lateral boundaries almost parallel at the base but strongly divergent towards the apex, the apico-lateral extremities distinctly less than rectangular but not pronouncedly acute and distinctly separated from the nearest compound eye. The supraclypeus about as prominent as the clypeus. The labrum slightly and rather evenly thickened, not tuberculate. The man-

dibles overlapping each other, wider at their base and their apex than they are at their middle, their apex with four teeth of rather uniform size, like those of *impunctata*. The malar space subtriangular, large on its outer half but narrowed inwardly, and at its shortest (near the inner angle of the mandible) about one-half the width of the flagellum. The labrum simple. The distance between the lateral ocelli (about twice the major axis of an ocellus) a little greater than that which separates each lateral ocellus from the nearest compound eye. The vertex somewhat carinate behind the ocelli. The front and the upper part of the sides of the face entirely dull and opaque owing to an exceedingly dense microscopic granular surface that utterly lacks shiny interspaces. The clypeus and adjacent parts of the sides of the face also very densely sculptured but a little more finely so, with a slight resulting sheen. The genal area with distinctly fine tessellation, almost or wholly sculptureless towards its lower extremity. The scape moderately robust, at its widest somewhat wider than the flagellum and about half the length of the latter. The head black with only a few obsolescent yellowish maculations, as follows: an obscure stripe along the lower one-half to two-thirds of the inner orbit of the eye, usually a crescentic maculation with the horns of the crescent pointing downward, in the supraclypeal area, and sometimes a very dull spot towards the middle of the apex of the clypeus. Ferruginous rather than yellow are the mandibles, except for their basal prominences and more vividly red apex; the labrum; the antennal sockets; a stripe in front on the scape and usually confined to its basal half; and the flagellum more or less beneath. Grayish, erect, medium-sized hairs on the front, vertex, and along the sides of the face; much more stunted erect gray hairs (visible only under a high magnification) on the clypeus; relatively long silvery gray hairs on the inferior one-third of the genal area; grayish to somewhat copper-colored, relatively long hairs fringing the inferior edge of the mandibles; and short pale hairs on the inner face of the scape. More conspicuous than the erect hairs are the silvery gray appressed hairs that are more especially concentrated on the front and sides of the face

but that occur also on the clypeus and on the upper two-thirds of the genal area.

THORAX: About as densely granular and lusterless as the front of the head; only on the propodeum is the sculpturing a little coarser and less crowded. The thorax relatively short; the width of the mesonotum at its widest, near the anterior margin, about as 7.5 is to 5.5 when compared with the length of the mesonotum. The length of the mesonotum and scutellum combined, when compared with the maximum width of the mesonotum, about as 8.5 is to 7.5. The backward extension of the rather flat scutellum, the posterior contour of which is almost hemispherical with occasionally a scarcely traceable emargination at the middle, is as great as that of the backward extension of the propodeum, which it over-roofs and tends to conceal when the insect is viewed from above. The tubercles almost horizontal in position. The erect hairs far more numerous and longer than in the known forms of *Paratrigona* other than *impunctata*. The mesopleura with fairly abundant, erect as well as appressed, silvery gray hairs. The mesonotum more sparsely and inconspicuously covered with grayish, sometimes in part even blackish, hair and the erect hairs of the scutellum (much longer than those of the mesonotum) at least largely or wholly black. The hairs on the mesosternum long and silvery gray. The silvery gray tomentum at each side of the bare middle area of the propodeum only a trifle denser than the tomentum on the mesopleura and metapleura. The thorax black and virtually without maculations: no bordering stripe such as is usual in all other *Paratrigona* along the sides of the mesonotum; at most a dull transverse stripe posteriorly on the pronotum, a very dull red spot on the axillae, an abbreviated dull red line on the apical tip of the scutellum (even these faint and shrunken vestiges of the pattern of maculation usual in *Paratrigona* sometimes absent in whole or in part).

LEGS: Robust, comparable to those of *impunctata*. The outer face of the front and middle tibiae and the inner face of the hind tibiae rather densely and very finely tessellated. The femora more or less shiny, usually polished on their anterior face but with their posterior face more or less thinly tessellated

to punctated; the outer face of the hind tibiae shiny almost from the base to the apex. The legs black to sometimes brownish, without maculations except that the apical joint at least of the tarsi is ferruginous. The hairs more abundant than in *Paratrigona* other than *impunctata*. There are silvery gray hairs on the coxae (especially long on the hind coxae anteriorly) and the under side of the trochanters (especially the middle and hind pairs), much shorter silvery gray hairs on the under side of the femora, and minute silvery gray appressed hairs over the outer face of the front and middle tibiae. The erect hairs of the tibiae and tarsi (except the more or less copper-colored metatarsal brushes on the inner face of the fore legs) are black: rather stunted and easily overlooked on the outer face of the fore tibiae, rather short also on the outer face of the middle tibiae, longer laterally on these tibiae, distinctly longer on the under side of the middle tibiae and on the outer face and laterally on the metatarsi, and a well-developed fringe along the anterior and the posterior lateral margins of the hind tibiae (fig. 55E), the hairs of the anterior margin sparser but somewhat the longer. There are also coarse black hairs on the middle and especially the hind femora above towards the apex.

WINGS: Almost clear and transparent, iridescent. The venation and stigma brownish, with the first transverse cubital vein rather clearly demarked; the second transverse cubital vein faint but traceable. The tegulae blackish with a dull reddish pupil. Of 16 lower wings examined, all had five hamuli.

ABDOMEN: Black. Tergites 1 and 2, in contrast to *Paratrigona* other than *impunctata*, largely smooth and polished, but with fine tessellation, interspersed sometimes with delicate punctures, along the apical one-third of tergite 2 and with far more feeble traces of tessellation (sometimes indeed absent) along the apex of tergite 1. Tergites 3 to 6 usually more or less telescoped, with only their daintily tessellated apical part revealed, but, when the abdomen is distended, the basal part of these tergites, too, reveals itself as smooth and polished. The tessellated apices of tergites 3 to 6, and to a lesser extent of tergite 2, covered with appressed grayish

hairs, and semi-erect grayish to occasional blackish hairs. The hairs of the venter as described for the subgenus.

MEASUREMENTS: Length about 4.5 mm.; width of thorax about 2 mm.; length of forewing, including tegula, about 4.5 mm.

QUEEN

Unknown.

MALE¹

HEAD: Wider than long, in the proportion of about 9.5 to 8, and nearly as wide as the distance measured from the outer rim of one of the tegulae to the outer rim of the other. The face very narrow, the distance from one eye to the other at their level of closest approximation (below) being about one-half of the length of the eye, whereas in the conspecific worker the shortest distance between the eyes is about five-sevenths the length of the eye. The distance that separates the eyes at their level of closest approximation about as 3.5 is to 5 when compared with the distance between them at the level just below the anterior ocellus, and about as 3.5 is to 7 when compared with the distance separating the anterior ocellus from the apex of the clypeus. The clypeus two-thirds as long as it is wide, rather strongly arched, hexagonal, the apex widely truncate along the middle and somewhat sharply receding to each side, the apicolateral angles not far from rectangular and virtually grazing the inner orbit of the eyes. The labrum simple. The mandibles somewhat thumb shaped in outline, rather wide at the base, running to a blunt point at the edentate apex, rather short, their tips meeting (but not overlapping), the inferior margin convex in outline towards the apex. The malar space represented by a minute vestigial subtriangular area below the outer one-half of the lower extremity of the eye, the inner angle of the base of the mandible being in contact or approximately in contact with the rim of the eye. The distance between the lateral ocelli about twice the major axis of an ocellus, and the distance between each lateral ocellus and the nearest compound eye about equal to the diameter of an ocellus. The region behind the ocelli somewhat raised.

¹ Description based on a single male from Muzo, Colombia.

The sculpturing of the head viewed from in front densely and finely granular, especially over the front, with resulting opacity, the clypeus and contiguous parts of the sides of the face with a little less crowded and somewhat more delicate sculpturing, and the sculpturing still less emphatic on the genal area, tending to be sparsely tessellate-punctate to smooth on the lower one-third of that area. The scape viewed from the side notably wider than the flagellum, which is nearly four times as long as the scape. The head black with the following light yellow maculations: a narrow stripe, somewhat widened below, along the inner orbit of the eye downward from a level somewhat below the anterior ocellus; a transverse stripe of irregular width fairly near to and parallel with the apex of the clypeus (this stripe somewhat reddened medianly). A stripe (also slightly reddened) extends down the front of the scape, the apical tip of the mandible is reddened, and the flagellum beneath is somewhat dull reddish brown. The hairs rather more numerous than in other known males of *Paratrigena* with the exception of *impunctata*. In contrast to the glabrous condition of the front in most males of this subgenus, *isopterophila* has numerous semi-erect, silvery gray to brownish hairs in this region in addition to the silvery gray appressed hairs that are present over the head viewed from in front to the inclusion of the clypeus, and also over all but the lower part of the genal area. The erect hairs on the vertex black, those fringing the lower edge of the mandibles and on the lower part of the genal area silvery gray.

THORAX: About as densely granular and lusterless as the front of the head; only on the propodeum is the sculpturing a little coarser and less crowded. The width of the mesonotum at its widest, near the basal margin, about as 7 is to 6 when compared to the length of the mesonotum and about as 7 is to 9 when compared to the length of the mesonotum plus the scutellum. The rather flat scutellum about three-fifths as long as it is wide; its posterior rim, with an ultrafeeble emargination at the middle, is widely hemispherical, extending backward so as to conceal or nearly conceal the propodeum when the insect is viewed from above. The tubercles almost horizontal in position. The

hairs more conspicuous than in other *Paratrigona* with the exception of *impunctata* and specimens of *lineata* from Lassance, Brazil. Only very short and appressed to barely semi-erect grayish hairs over the mesonotum; still very short but erect silvery gray hairs on the mesopleura; long blackish hairs on the scutellum, particularly along the posterior margin, in addition to short appressed silvery gray hairs; long silvery gray hairs on the mesosternum. The propodeum bare on the large dorsal and middle area, but flanked on

silvery gray sericeous appressed microscopic hairs such as occur also on the posterior face of the several femora, with the addition of a few semi-erect short blackish hairs on the anterior face of the hind femora near the apex. The under side of the fore and especially the middle tibiae with a few erect black hairs. Very inconspicuous, more or less blackish stunted hairs along the anterior and posterior lateral contours of the hind tibiae, those of the posterior lateral contour a little the shorter. A few hairs of intermediate

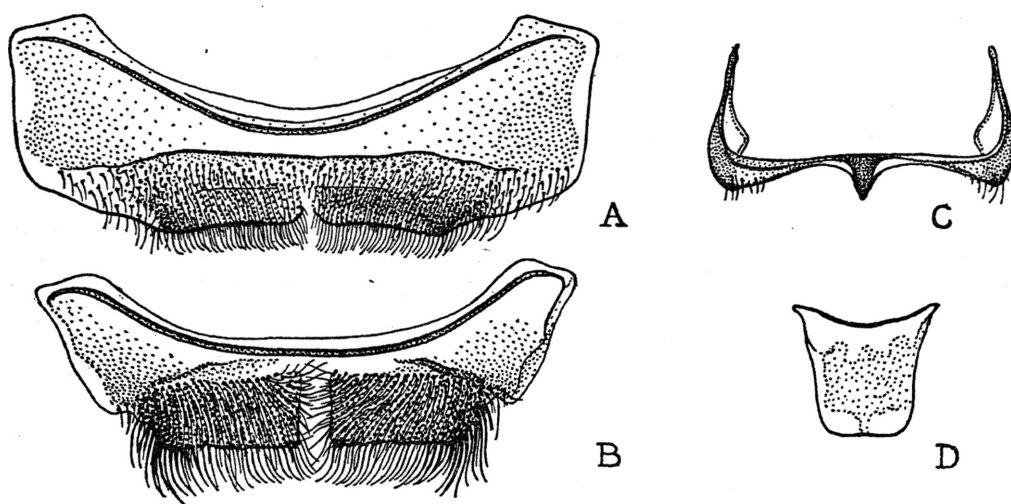


FIG. 65. Abdominal parts of male of *Trigona* (*Paratrigona*) *isopterophila* Schwarz. A. Sternite 4. B. Sternite 5. C. Sternite 6. D. Sternite 7. All based on a specimen from Muzo, Colombia. Drawings by Shirley H. Risser.

each side by a dense patch of silvery gray tomentum. The thorax black.

LEGS: With tessellation far more delicate than that of at least the head and thorax. The anterior face of the fore and middle femora polished, hairless, and shiny. The legs blackish to brownish, with the small joints of the tarsi, and more especially the apical joint, reddish; the tibiae without maculations in agreement with *impunctata* but in contrast to most *Paratrigona*. The erect hairs fewer and more stunted than in the conspecific worker. Silvery gray erect hairs are present on the coxae and trochanters beneath but short in both cases. The femora have a microscopic fringe of pale hairs on their under side, but the outer face of the fore and middle tibiae is devoid of erect hairs, having only

length on the outer face of the fore metatarsi, but the metatarsi of the middle and hind legs with only appressed hairs on their outer face. The metatarsal brushes dull golden on the fore legs, copper colored and at some angles silvery on the hind legs.

WINGS: Almost clear and transparent, iridescent. The venation and stigma brownish to blackish, with the first transverse cubital vein rather clearly demarked, the second fainter. The tegulae blackish, immaculate. The number of hamuli per lower wing five.

ABDOMEN: Black. Tergite 1 smooth and polished except for very delicate traces of tessellation at the apex; tergite 2, contrary to the condition in the worker, and contrary, too, to the condition in the male of the closely related *impunctata*, with very fine

sculpturing on the basal two-thirds (with the result that this area is not quite smooth) in addition to delicate tessellation on the apical one-third. The apex of the subsequent tergites with tessellation stronger than that of the corresponding areas of the worker from the same region but less pronounced than the tessellation of the head and thorax. The basal part of these tergites, when exposed, also proves to be tessellated, even if very lightly, in contrast to the polished bases (usually concealed) of these tergites in the worker. Tergites 2 to 6 with dark grayish to blackish, for the most part appressed hairs in their apical region, corresponding with the area of stronger tessellation. Tergite 7 fringed apically with rather long black hairs. The venter silvery gray tomentose over the apical half of sternites 1 to 5, almost plush-like on the exposed parts of sternites 3 to 5. The structure of the sternites virtually duplicates the condition in *impunctata*. Sternite 4 is depressed widely over the middle region; its apex with an even somewhat narrower and shallower emargination at the middle than that of *impunctata* but in other respects like that form, with a truncation that is terminated at each lateral extremity with a small, almost nipple-like prominence; the apical truncation fringed with hair from end to end. Sternite 5 likewise widely depressed over its middle region; its apex, with a rather rectangular emargination at the middle that is notably wider and deeper than the emargination of sternite 4, is otherwise truncate from end to end and fringed throughout with hairs that are longest and coarsest at the lateral extremities; these lateral extremities shoulder-like and prominent, being visible even when the bee is viewed from above. Sternite 6 with a short, stout, triangular, median spine, the tip of which terminates at approximately the same level as the shoulder-like lateral termini of the sternite. (Fig. 65.)

MEASUREMENTS: Length about 4.5 mm.; width of thorax about 2 mm.; length of forewing, including tegula, about 4.5 mm.

TYPE MATERIAL

Holotype and paratypes from Barro Colorado, Canal Zone, in the American Museum of Natural History, and paratypes in the collection of T. D. A. Cockerell.

DISCUSSION

Trigona (Paratrigona) isopterophila is so close to *impunctata* that I originally described it merely as a subspecies of that species. But, in addition to having more limited maculation and usually darker hairs than *impunctata*, it is separable also structurally by its more developed scape. On the other hand, its close affiliation to *impunctata* is emphasized not merely by its essential identity with that insect in nearly all of its plastic characters (to the inclusion even of identity of structure in the abdominal sternites of the male¹) but also by its mode of life, for it, too, is known to build in termite colonies, as the following observation of C. H. Curran, the collector of *isopterophila*, makes clear:

"The nest of this interesting *Trigona* was found in a deserted termite nest on a small palm tree having a circumference of about eighteen inches. The termite nest was small, about a foot high and approximately eight inches across, and located between eight and nine feet from the ground. In the face of the nest, that is to say in the surface opposite the axis of the palm trunk, was the entrance to the *Trigona* nest, a small hole, large enough for the passage of only one insect at a time.

"On some occasions while the nest was under observation the bees were returning at the rate of approximately two a minute, but as a general rule only about half this number were observed. The peculiar attraction of the domicile was due to the habits of the bees, particularly the presence of a door-keeper, a habit I had not previously observed, although the phenomenon has not passed unnoticed by others. While there was no activity, the head of the guardian completely filled the entrance and as a result it was apparent only under close scrutiny and in good light, and it would easily have passed unnoticed had its presence not been known or attention attracted to it by the returning and departing bees. As a returning bee neared the nest, the head of the door-keeper would disappear and there was no loss of time in the entrance of the worker. Rarely did the re-

¹ This statement applies particularly to the distinctive sternites 4 to 7. The genitalia of the single specimen of *isopterophila* on which above description is based are unfortunately too fragmentary to permit of satisfactory comparison with those of *impunctata*.

turning bee find it necessary to alight before the guardian's head would disappear from the opening and, no sooner had the worker entered, than the entrance was once more blocked. Unfortunately, the nest was too high above the ground to determine whether the same bee acted as guard continuously, but the alacrity with which it performed its duties would seem to indicate that this was so for at least a considerable period. The nest was evidently a small one and only a few bees were captured" (cited by Schwarz, 1934, pp. 21-22).

In addition to the type material there is before me also a worker collected by J. Bequaert in 1936 at Muzo, Department of Boyacá, 900 meters, Colombia. Because of its more developed scape and more restricted maculations this individual groups itself with *isopterophila*, although it departs slightly from the type material of that species in having the mandibles black, with an apical stripe of red, instead of ferruginous basally as well as apically. Also, in contrast to the type material, it has a well-developed stripe on the scape. Nevertheless, these distinctions do not seem sufficiently striking to justify its separation as a variety of *isopterophila*.

The male, likewise obtained at Muzo by Bequaert, in respect to the immaculate condition of its thorax approximates the worker of *isopterophila*, but in its facial markings it more nearly resembles *impunctata*. As pointed out in the description, the abdomen of the male of *isopterophila* is not only more strongly tessellated than that of the worker but the tessellation extends to areas that in the worker are polished. In this respect the male of *isopterophila* parallels a condition noted in the males of certain of the other species of this subgenus—for instance, *lineata* and *petropolis*.

DISTRIBUTION

Described from Barro Colorado Island, Canal Zone, where it was collected by C. H. Curran, January 10, 1929, and by F. E. Lutz, December 3, 1930.

COLOMBIA: Department of Boyacá: Muzo, 900 meters, males as well as worker (J. Bequaert).

TRIGONA SUBGENUS SCHWARZIANA (MOURE)

Schwarziana MOURE, 1943, p. 147.

TYPE SPECIES: *Melipona (Trigona) quadripunctata* Lepeletier.

WORKER

DIAGNOSTIC CHARACTERS: Especially differentiated from the other subgenera of *Trigona* by the following combination of characters: Head, thorax, and tergites of abdomen finely and densely tessellated. The lower half of face maculated. The propodeum somewhat longer than the scutellum, densely tessellated, and with hairs on its dorsal middle as well as its sides. The hind tibiae with a corbícula extending from the apex almost to the base, but shallow and flat throughout its extent. Under side of hind tibiae unevenly gabled. Hairs fringing posterior rim of hind tibiae unbranched. Number of hamuli rather large for a *Trigona*, ranging from seven to 10 per lower wing.

HEAD (FIG. 66A): Finely and densely tessellated, a little less opaque on the clypeus and lower part of genal area. Head wider than long, extending to each side slightly beyond the outer rims of the tegulae. The eyes somewhat convergent below, the ratio between the intervening space at their upper extremity and the intervening space at their lower extremity being about as 7 is to 6. The clypeus arched and, as is the triangular supra-clypeus, more prominent than the sides of the face, three-fifths as long as its greatest width, hexagonal, with the apex rather widely truncate medianly but sharply receding towards each of its lateral extremities, which form an angle of about 90° at their point of contact with the diagonally directed sides. The labrum simple. The mandibles (fig. 66A) somewhat hourglass shaped with their apical edge edentate over its outer two-thirds to three-fourths but with two denticles at the inner extremity. The malar space short but distinct, about one-half as long as the scape is wide. The lateral ocelli raised somewhat above the level of the rest of the head and tilted outward, each distant from the nearest compound eye by about the distance from the outer rim of either lateral ocellus to the farther rim of the middle ocellus, which is a little less than the distance separating the lateral ocelli. The region behind the ocelli slightly thickened. The flagellum about twice as long as the scape. The lower half of the face maculated but not the upper half. Head distinctly hairy, the erect hairs being rather coarse and thick and even

subplumose, shorter on the clypeus than the scape is wide but increasing in length on the upper half of the face to attain the maximum length on the vertex. The hairs on the genal area likewise erect or semi-erect and moderately dense, somewhat short above but increasing much in length downward. Rather long hairs fringing the lower margin of the mandibles; much shorter hairs on the labrum.

tions, but not the mesonotum. Thorax rather hairy, as is the head, with the hairs of the scutellum somewhat longer than those of the mesonotum, and the hairs on the mesopleura and under part of thorax long and dense.

LEGS: With the tessellation feeble to more or less absent. The middle leg intermediate in length between the short fore leg and long hind leg, which is about as long as the

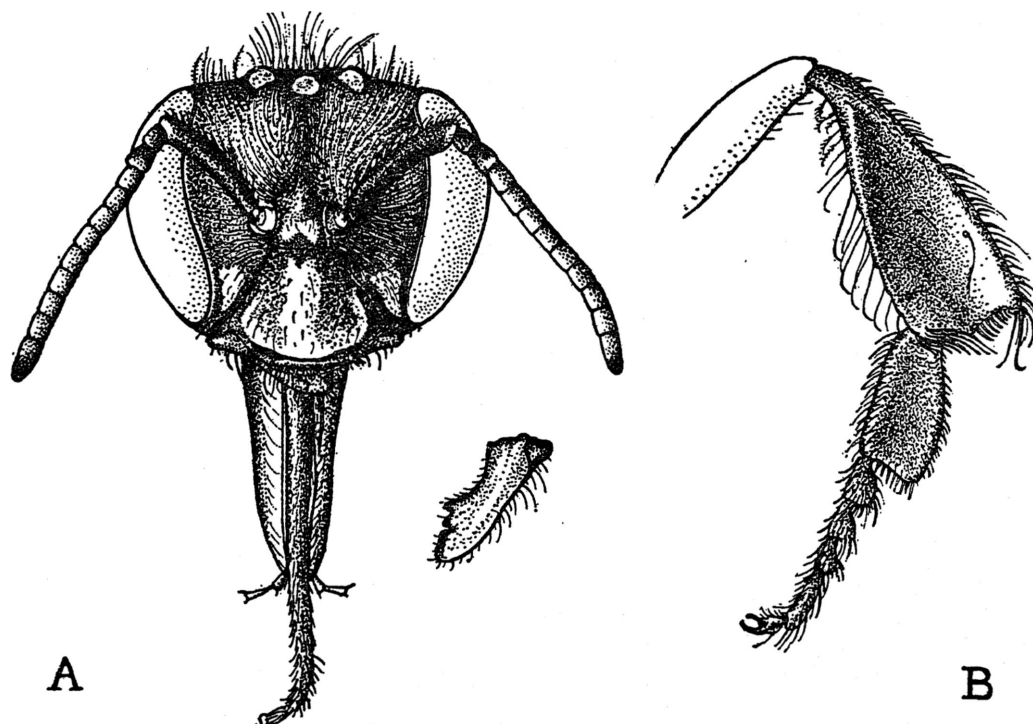


FIG. 66. Worker of *Trigona* (*Schwarziana*) *quadripunctata* variety *quadripunctata* (Lepelletier). A. Head and mandible. B. Tibia and tarsal joints of hind leg. Drawings by Shirley H. Risser.

THORAX: Finely and densely tessellated on the mesonotum, which is slightly wider than long; a little more coarsely and sparsely tessellated on the mesopleura. The scutellum finely and rather densely tessellated, short, rounded posteriorly, not extended backward over the propodeum. The propodeum somewhat longer than the scutellum, densely tessellated, with the tessellation a trifle larger on the dorsal area than on the sides. The propodeum somewhat hairy in its dorsal middle as well as distinctly so on its sides, where the hairs tend to be long. The pronotum, usually the axillae, and the scutellum with macula-

combined length of the head, thorax, and abdomen. The fore tibiae shorter than their femora; the middle tibiae hardly as long as their femora; the hind tibiae about as long as their femora plus their trochanters. The hind tibiae (fig. 66B) somewhat club shaped in outline, with their anterior and posterior contours convex; the apical edge irregular, with a small anterior angle followed by a convexity, which is in turn succeeded by an emargination terminating in a stronger angle at the posterior end. The exterior face of the hind tibiae notable in that the corbicula, like that of *Partamona* and *Parapartamona*, ex-

tends from the apex almost to the base, but it is not deeply hollowed as in those subgenera, being distinctly flat. The hind tibiae about two and one-half times as long as they are wide, their width only about one-third greater than that of the posteriorly rounded hind metatarsi. The hairs are much longer on the under side than on the upper side of at least the fore and middle femora. The rather dense hairs on the outer face of the fore and middle tibiae very short, only semi-erect, those of the fore tibiae being, if anything, longer than those of the corresponding area of the middle tibiae. The hairs on the sides and internal face of these tibiae emphatically longer, especially those of the middle tibiae. Simple eyelash-like hairs fringing the anterior and posterior contour of the hind tibiae. The inner face of the hind tibiae unevenly gabled, with rather coarse, dense, semi-erect hairs along the ridge and dense, microscopic, silvery gray appressed hairs over the sloping surface behind the ridge.

WINGS: Very long and with from seven to 10 hamuli per lower wing, but very exceptionally with as few as seven or as many as 10. The transverse cubital veins obsolescent rather than obsolete, the first transverse cubital vein being clearly, if feebly, chitinized. The first discoidal cell barely shorter than the marginal, about eight-ninths as long.

ABDOMEN: Nearly as wide as the thorax and rather oval in shape, dull owing to the extent and character of its sculpturing. Tergite 1 finely and densely tessellated but in addition usually with more or less blotchy punctures, especially at the apex medianly. The tergites beyond tergites 1 with a relatively narrow, basal, hairless strip (frequently concealed) that has such light tessellation that it appears almost smooth and shiny, but the much more extensive region apicad is hairy, tessellated, and vaguely punctate as well. The hairs on tergite 1 considerably longer and more erect than those of the subsequent tergites. The hairs on tergites 2 to 4 semi-appressed, short, and somewhat coarse. Those on tergites 5 and 6 longer, particularly so on tergite 6, and spine-like. The under side of the abdomen punctate-tessellate, with the tessellation rather finer and the punctation stronger than is the case on the

upper side. The sternites (except for a narrow, usually concealed, basal strip) densely covered with erect silvery gray hairs that are much longer than the hairs on tergites 2 to 5 and tend to be plumose.

MEASUREMENTS: Length 5.5 to 6.5 mm.; width of thorax 2.25 to 2.5 mm.; length of forewing, including tegula, about 7 mm.

QUEEN

See the description under *quadripunctata* variety *quadripunctata*.

MALE

DIAGNOSTIC CHARACTERS: Differs from males of the other subgenera of *Trigona* through the following combination of characters: Chitin of head, thorax, and tergites of abdomen densely and finely tessellated. The lower half of the face maculated but not the upper. The propodeum densely tessellated, barely longer than the scutellum, and lightly hairy over its dorsal middle as well as more densely so at its sides. The number of hamuli rather large for a *Trigona*, variable from seven to nine per lower wing. Differs from all other known male *Trigona* of New World in having on sternite 3 a conspicuous crescentic fimbria of erect hairs just above an area of dense soft tomentum and on the apex of sternite 4 a fringe of forward-pointing, almost spine-like hairs.

HEAD (FIG. 67A): Finely and densely tessellated, wider than long, extending to each side somewhat beyond the outer rim of the tegulae. The eyes large and distinctly convergent below, the ratio between the intervening space at their upper extremity and the intervening space at their lower extremity being about as 6.5 is to 5. The clypeus fully three-fifths as long as its greatest width, hexagonal, with the apex rather widely truncate but sharply receding at each of its lateral extremities, which form an angle of barely more than 90° at their point of contact with the diagonally directed sides. The labrum simple. The mandibles (fig. 68) slightly overlapping, about twice as wide at the base as at the apex, the narrow apical edge slightly emarginate to very nearly truncate. The malar space somewhat shorter than in the worker. The ocelli markedly elevated, the lateral ones tilted outward and separated

each from the nearest compound eye by a space approximating one and one-half times the major axis of an ocellus, the separating space being less than in the worker and less also than the distance between the lateral ocelli. The flagellum a little narrower than the scape and about four times as long; joint

is wide, and on the mesopleura. The scutellum finely and rather densely tessellate, short, rounded posteriorly, not extended backward over the propodeum. The propodeum somewhat longer than the scutellum, densely tessellated, with the tessellation somewhat larger on the dorsal surface than

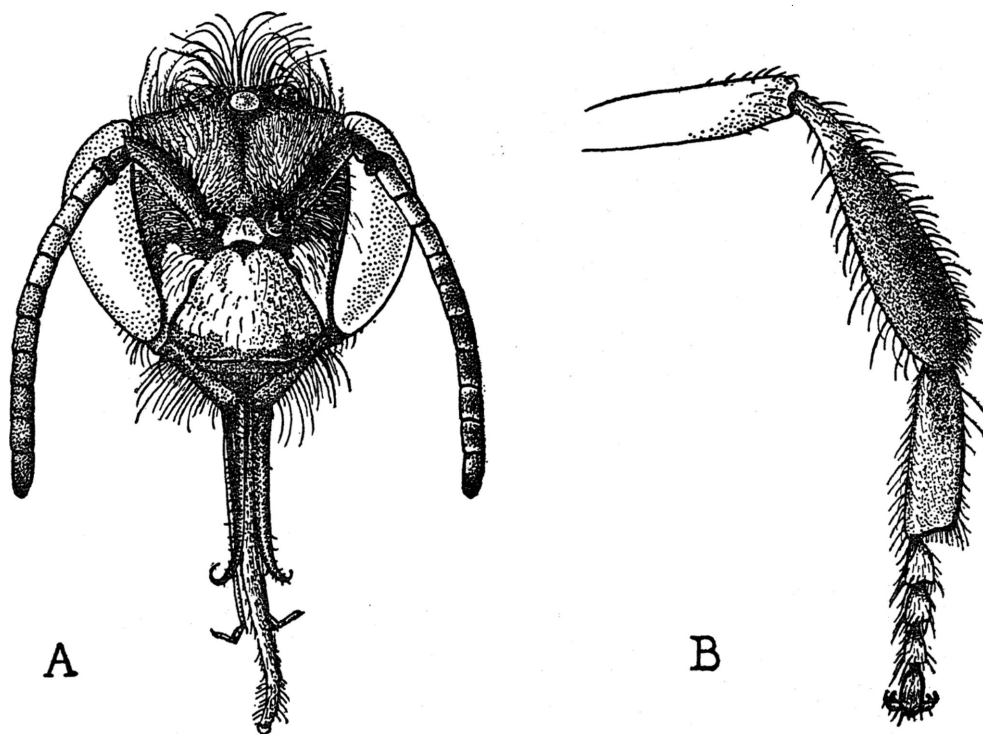


FIG. 67. Male of *Trigona* (*Schwarziana*) *quadripunctata* variety *quadripunctata* (Lepelletier). A. Head. B. Tibia and tarsal joints of hind leg. Drawings by Shirley H. Risser.

3 of the flagellum viewed from above a little shorter than joints 1 + 2 but viewed from below distinctly longer than the combined length of these joints. The lower half of face maculated but not the upper. Head distinctly hairy, the hair shorter on the clypeus than the scape is wide but emphatically longer on the front and vertex; the hairs on the genal area of rather even density, those towards the lower part of the area being longer than those towards the upper part. The labrum with relatively short hairs, but the hairs bearding the inferior edge of the mandibles very long, the longer hairs being distinctly longer than the mandible is wide at the base.

THORAX: Finely and densely tessellated on the mesonotum, which is about as long as it

on the sides. The propodeum somewhat hairy over its median dorsal portion, but the hairs of this region not so long or dense as those of



FIG. 68. Mandible of male of *Trigona* (*Schwarziana*) *quadripunctata* variety *quadripunctata* (Lepelletier). Drawing by Alice Gray.

the sides of the propodeum and sometimes sparse. The pronotum, axillae, and the scutellum usually with maculations; the mesonotum with or without a lateral stripe. Thorax hairy like the head, with the hairs of the

scutellum somewhat longer than those of the mesonotum and the hairs on the mesopleura dense and long.

LEGS: With the tessellation more feeble. The middle legs somewhat intermediate in length between the short fore leg and long hind leg, which approximates in length the combined length of head, thorax, and abdomen. The combined tarsal joints of the middle legs fully as long as the combined tarsal joints of the hind legs, the middle metatarsus being nearly as long as the middle tibia. The hind tibiae (fig. 67B) very gradually expanded from base to apex, the apex being rounded anteriorly and very slightly angulate posteriorly. These tibiae narrower than those of the worker and not flattened on their external surface but gently convex; the inner surface constructed much like that of the worker, with an uneven gable resulting in a short, steep, anterior part and a larger, more gently sloping, posterior part. The hind metatarsus a trifle more than one-half as long as the hind tibia and a little narrower, its sides approximately parallel, a little convergent towards the base. The combined length of the hind metatarsus and the small joints of the tarsi distinctly greater than the length of the hind tibiae. The hairs tend to be longer on the under side of the fore and middle femora than on the upper side, but longer on the upper side of the hind femora than on the under side. The hairs on the outer face of the fore tibiae short but longer, nevertheless, than the very stunted microscopic hairs on the outer face of the middle tibiae; the fore tibiae with fairly long hairs fringing them posteriorly and the middle tibiae with fairly long hairs posteriorly and on their under side. The hind tibiae with many erect to semi-erect hairs over their outer face and also fringing the anterior and posterior contours. The gabled inner face of these tibiae with erect or semi-erect bristles on the anterior slope and dense, appressed, silvery gray, microscopic hairs on the posterior slope.

WINGS: Like those of the worker, the stigma sometimes barely darker; from seven to nine hamuli per lower wing.

ABDOMEN: Nearly as wide as the thorax and rather oval in shape, dull over the tergites owing to dense and fine tessellation. Tergite 1 with erect, fairly long hairs, more

especially on its upper half around the lightly depressed basal concavity. The subsequent tergites with very short, semi-appressed hairs except for tergite 7, which is fringed with fairly long hairs, and along the lateral edges of tergites 4 and 5 there are also such fringing hairs even if these are shorter. The under side of the abdomen with far lighter sculpturing and more shiny. Sternites 1 and 2 merely silvery gray sericeous but sternite 3, hairless basally and shiny, has on its apical half a conspicuous crescentic-shaped fimbria of stiff erect hairs that arches above an area of dense, soft, plush-like tomentum. Sternite 4 medianly emarginate with a fringe of bristle-like hairs along its apex that point forward towards the fimbria. Sternite 5 likewise emarginate medianly. Sternite 6 with a median spine that is distinct in outline notwithstanding the fact that it is frequently more or less surrounded (except for its tip) by a thin layer of almost transparent chitin. (See fig. 69A-G.)

MEASUREMENTS: Length 5.5 to 7.5 mm.; width of thorax 2.25 to 2.5 mm.; length of forewing, including tegula, about 7 mm.

DISCUSSION

Ducke (1925, p. 355) in his key to Brazilian Meliponidae placed *quadripunctata* between his Group V, which contains certain members of the subgenera *Partamona*, *Trigona*, and what Moure has separated as *Geotrigona*, and his Group VI, which is *Melipona* in the limited sense. He placed *quadripunctata* particularly close to *subterranea* Friese, belonging to Moure's group *Geotrigona*. Members of *Schwarziana* resemble *subterranea* and closely allied forms like *mombuca*, *fulvohirta*, etc., in their hairiness, rather notably long wings, and the relative clarity of the transverse cubital veins of those wings, which are obsolescent rather than obsolete. However, even with respect to the wings *Schwarziana* is distinctive in having a larger number of hamuli. In certain other rather fundamental respects *Schwarziana* does not seem closely allied to *subterranea* and its allies. Its tessellated integument differentiates it somewhat sharply from the smoother chitin of these insects, but equally important is the wholly different structure of its hind leg. The hind tibiae are distinct from those of *subterranea*

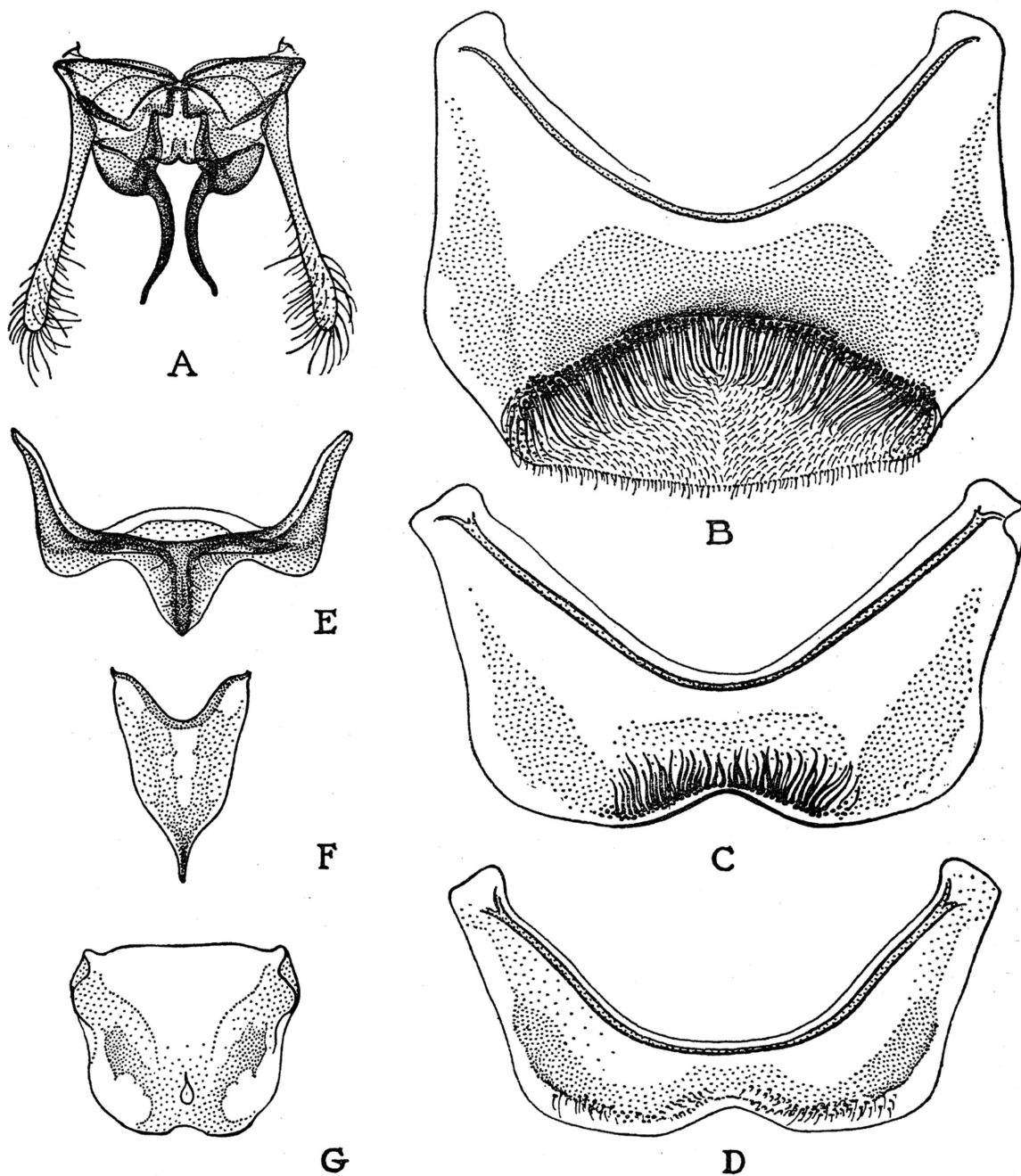


FIG. 69. Abdominal parts of the male of *Trigona* (*Schwarziana*) *quadripunctata* variety *quadripunctata* (Lepeletier). A. Genitalia (chitinated parts only). B. Sternite 3. C. Sternite 4. D. Sternite 5. E. Sternite 6. F. Sternite 7. G. Membranous segment that occurs within tergite 7. All parts based on a specimen from Santa Catharina, Brazil. Drawings by Shirley H. Risser.

and its allies in their contour and in the extent of the corbicula and also rather fundamentally in the structure of their inner face. This inner face is arched or, more accurately, unevenly gabled in *Schwarziana*. In contrast, *subterranea*, like other members of *Geotrigona* Moure, and like members also of the subgenera *Trigona* and *Tetragona*, of which in my estimation *Geotrigona* is hardly more than a division, has the median area of the inner face of the hind tibiae abruptly raised into a sort of plateau-like elevation that contrasts with the flatness of the bordering area. *Tetragona* like *Trigona* has plumose as well as simple hairs fringing the hind tibiae posteriorly. In *Schwarziana* the hairs of the hind tibiae are simple.

In my estimation the subgenus *Schwarziana* is of a rather generalized type, suggesting affiliations with several of the other subgenera. In respect to its tessellated propodeum, the hairiness of its thorax, the oval shape of its abdomen, the structure of the inner face of the hind tibiae, and the relatively large number of hamuli per lower wing it is *Melipona*-like and, in the probability that *Melipona* is more primitive than *Trigona*, may be regarded as a not very advanced derivative from *Melipona*.

Schwarziana seems to me in turn possibly ancestral to *Parapartamona*, the sculpturing of which it so closely approximates. Although the excavated external face of the hind tibiae of the worker is much flatter and distinctly less capacious in *Schwarziana* than in the deeply hollowed hind tibiae of workers of the subgenera *Parapartamona* and *Partamona*, the area of excavation is about equally great in all three subgenera and *Schwarziana* represents possibly the first stage of a progressive series of which *Partamona* is the culmination. The presence of hairs in the usually hairless middle region of the propodeum is another character which links *Schwarziana* with the other two, more advanced subgenera, but this character is also *Melipona*-like.

The sculptured chitin is a character that *Schwarziana* shares not only with *Parapartamona* but also with *Paratrigona* and certain *Hypotrigona*.

Ducke's contention (1925, p. 426) that *Schwarziana* has as its nearest relative sub-

terranea seems to be based in part on the fact that both construct nests in the earth, but it is to be recalled that *Partamona*, which I suggest may be in line of descent from *Schwarziana*, is also sometimes an earth dweller. The nest of *Parapartamona* is unknown.

All the colonies of *Schwarziana* referred to in the literature (F. Smith, 1868, p. 134; H. von Ihering, 1903, pp. 227-228; Marianno, 1911, pp. 123-124; Bertoni, 1911, p. 142; Ducke, 1925, p. 426) were subterranean. The depth at which the nests were located ranged from 30 to 50 cms. (Bertoni) to 3 meters (H. von Ihering). The nest observed by Bertoni had no entrance spout, but those described by von Ihering (one of which, at least, was shaped like "a baking oven or a half of an orange") and which contained in the one case seven, in the other case eight spirally arranged combs, had an orifice measuring from 10 to 17 mm. in diameter. Ducke (1925, p. 426) gives the following summary: "Nest. According to Ihering (1903) and J. Marianno deep in the earth; flighthole simple or with a tube fashioned of earth; brood envelope greatly developed; combs as a rule spirally arranged; royal cells not observed, but nevertheless doubtless present; provision containers around outer circumference of the brood mass, of more than medium size, not much higher than wide; honey scant but pleasant to the taste. Bees timid."

To this should perhaps be added that Marianno (1911, p. 81) surmised that the nest site might be a deserted fornicary of *Atta sexdens*.

KEYS TO THE VARIETIES OF *Trigona* (*Schwarziana*)

WORKERS

1. The abdomen black or blackish both dorsally and ventrally. *quadripunctata* variety *quadripunctata* (Lepeletier)
The tergites of the abdomen predominantly reddish yellow beyond tergite 1, which is sometimes reddish yellow but, more often, black or blackish *quadripunctata* variety *bipartita* (Lepeletier)

QUEENS

(Only the queen of the typical variety has come to my attention.)

MALES

1. The abdomen black or fuscous *quadripunctata* variety *quadripunctata* (Lepeletier)
The tergites of the abdomen more or less blackish medianly but flanked, at least, with reddish yellow (callosity condition?), and often more or less cloudy reddish to yellowish apically
quadripunctata variety *bipartita* (Lepeletier)

Trigona (Schwarziana) *quadripunctata* variety *quadripunctata* (Lepeletier)

Melipona (*Trigona*) *quadripunctata* LEPELETIER, 1836, p. 430.

Trigona quadripunctata, F. SMITH, 1854, p. 409.

Trigona quadripunctata, HOLMBERG, 1887, pp. 280-283.

Melipona quadripunctata, DALLA TORRE, 1896, p. 583.

Trigona quadripunctata, HOLMBERG, 1903, p. 377.

Trigona quadripunctata, H. VON IHERING, 1903, pp. 227-228, 237, 243, 249.

Trigona quadripunctata, GRÜNBERG, 1904, pp. 9, 10.

Trigona quadripunctata, STRAND, 1909, p. 235 (identified by H. Friese).

Trigona quadripunctata, STRAND, 1910, p. 559.

Trigona quadripunctata, BERTONI, 1911, p. 142.

Trigona quadripunctata, MARIANNO, 1911, pp. 40, 123-124.

Melipona quadripunctata, DUCKE, 1916, p. 26, opposite p. 28, pp. 139-141, pl. 7, fig. 22.

Melipona quadripunctata, DUCKE, 1925, pp. 341, 344, 355, 424-426, text fig. Z, pl. 4, fig. 22.

Melipona quadripunctata, BISCHOFF, 1927, pp. 287, 290, 291, 293.

Melipona quadripunctata, ALFKEN, 1932b, p. 306.

Trigona quadripunctata, SCHWARZ, 1932a, pp. 259, 282.

Trigona quadripunctata, MAIDL, 1934, pp. 578, 581.

Trigona quadripunctata, R. VON IHERING, 1940, p. 62.

Trigona (Schwarziana) *quadripunctata*, MOURE, 1943, p. 147.

Melipona quadripunctata, DUCKE, 1945, p. 23, opposite p. 24, pp. 105-107, pl. 7, fig. 22.

WORKER

DIAGNOSTIC CHARACTERS: Chitin of abdomen black or fuscous.

HEAD (FIG. 66A): Black throughout except for a yellowish maculation of somewhat variable extension (usually of an inverted T shape) on the clypeus (see discussion), a

small supraclypeal maculation, a triangle at each side of the clypeus in the space between the clypeus and the inner rim of the compound eye, and sometimes a small maculation at the lower extremity of the genal area. The labrum more or less black and the mandibles more or less cloudy reddish, or largely black with only the apex reddened (specimens from Nova Teutonia). The hairs on the genal area and labrum silvery gray. The hairs fringing the lower margin of mandibles ferruginous to brown. The short erect hairs on the clypeus vary from wholly silvery gray through intermixed silvery gray and black, with silvery gray predominating, to wholly black (even among specimens from a single locality, Passa Anatro, diversity occurs). The hairs of the vertex black and at least the upper half of the front with more or less black hair that may, however, extend downward, displacing in part or entirely the silvery gray hairs that are sometimes present over the lower half of the front. Scape black; flagellum black above and ferruginous, fuscous, or wholly black below.

THORAX: Black, but with the following areas yellow: a transverse stripe, medianly interrupted, across the posterior half of the pronotum; the axillae; and a half circle bordering the posterior rim of the scutellum and usually briefly interrupted or narrowed at its middle. The hairs on the mesonotum and scutellum black except that sometimes there are horizontally located, silvery gray hairs fringing the hind margin of the scutellum. The hairs on the mesopleura variable from black through pale coffee color to silvery gray (specimen from Bompland). Tomentum on propodeum silvery gray.

LEGS: Brownish to blackish, with the hairs silvery gray on the coxae, trochanters beneath, and the femora. The hairs are black on the outer and inner face of the fore and middle tibiae, along the anterior and posterior contours of the hind tibiae, and on the outer face of the metatarsi and of the subsequent tarsal joints. The bristles on the crest of the arch of the inner face of the hind tibiae black or blackish; the dense microscopic hairs on the posterior slope of the inner face silvery gray. The metatarsal brushes and the inner face of the small joints of the tarsi golden to sometimes copper colored.

WINGS: Subhyaline, slightly suffused with yellowish, their venation and stigma rather bright ferruginous. Number of hamuli per lower wing, in the 50 wings examined, varied from eight to 10. Of these, 22 had eight hamuli, 26 had nine hamuli, and two had 10 hamuli, an average of 8.64. Tegulae deep cloudy reddish to fuscous with usually a reddish pupil.

QUEEN (GRAVID)¹

HEAD (FIG. 70A): Finely and densely tessellated, scarcely less densely than that of the worker, with the lower end of the sides of the face and the lower extremity of the genal area devoid of tessellation but with occasional punctures on an otherwise mainly smooth surface. Head actually somewhat smaller and, when compared to the width of the thorax,

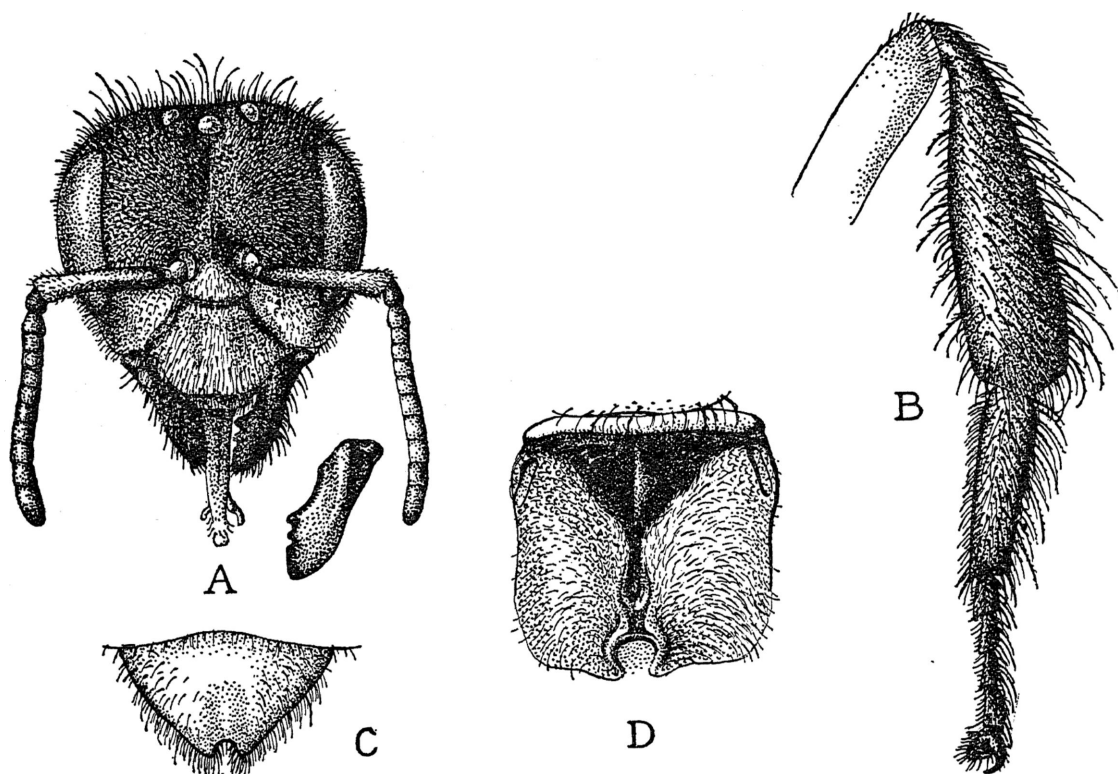


FIG. 70. Queen of *Trigona* (*Schwarziana*) *quadripunctata* variety *quadripunctata* (Lepelletier). A. Head. B. Tibia and tarsal joints of hind leg. C. Sternite 6 of abdomen. D. Propodeum.

ABDOMEN: Black or fuscous, with the hairs of tergite 1 silvery gray and the subsequent tergites also sometimes with largely silvery gray hairs, but usually there are black hairs as well, more especially on tergites 3 to 6 apico-laterally, and sometimes these black hairs have largely or completely replaced the silvery gray hairs. The hairs on the sternites silvery gray except for the last visible sternite, the hairs of which are sometimes black.

MEASUREMENTS: Length 5.5 to 6.5 mm.; width of thorax 2.25 to 2.5 mm.; length of forewing, including tegula, about 7 mm.

relatively very much smaller than that of the worker, the width of the head compared to the distance from the outer rim of one of the tegulae to the outer rim of the other being about as 10.5 is to 14. The eyes, about three-fourths as long as those of the worker and about two-thirds to three-fourths as wide, are very slightly divergent below (about as 7.5 is to 7 when compared to the distance separating them near the summit). The somewhat arched clypeus rising a little

¹ Description based on a single specimen from Nova Teutonia, Brazil.

above the sides of the face, about three-fifths as long as its greatest width, hexagonal, with the apex rather widely truncate medially but sharply receding towards each of its lateral extremities, which form approximately a right angle at their point of contact with the diagonally diverging sides. The supraclypeus fully as prominent as the clypeus and resembling that of the worker, rather triangular in contour, its summit strongly carinated and pointed towards the middle ocellus, with which it is connected by a rather deep fossa. The labrum simple. The mandibles (fig. 70A) widest at the apex and at the base, with a slight "waist" towards the middle; their apical edge edentate on the outer two-thirds to three-fourths but with two denticles on the inner one-fourth to one-third. The malar space much longer than in the worker, its length approximating twice the width of the flagellum. The ocelli distinctly smaller than those of the worker, the middle ocellus only barely anterior to the lateral ones, which are tilted each towards the nearest compound eye; the distance between the lateral ocelli a little less than the distance between a lateral ocellus and the nearest compound eye. The region behind the ocelli slightly thickened. The flagellum about as wide as the scape and about twice as long. The head black with reddish¹ rather than, as in the worker, yellowish maculations, and these confined to the lower half of the head. The maculation on the clypeus extends over virtually the entire surface, with only a minimum of black surviving on each side of the basal middle of the clypeus feebly to suggest the inverted T which is the usual shape of the maculation in the worker from the same nest. The side-facial maculations do not quite fill the space between the clypeus and the eye, their upper boundary slightly above the base of clypeus but their lower part extended downward and outward over the malar space. The maculation in the supraclypeal area triangular to trapezium shaped without an emargination below. The labrum is of a much darker red than the light red clypeus. The mandibles,

¹ Ducke, on the other hand, described (1925, p. 425) the entire lower half of the face of the queen as an "attractive yellow," and it is likely that the maculations of the queen vary in intensity and clarity from specimen to specimen.

too, are dark red except for their narrow apical edge of black and the black basal prominences. The flagellum feebly reddened below. The hairs for the most part of different color and of different relative length from those of the corresponding areas of the worker. The longer hairs of the clypeus are stramineous and are coarser and longer than the hairs on the clypeus of the worker, but in addition to these longer hairs there are semi-appressed, short, silvery gray hairs in this area and on the supraclypeus and labrum. The front is entirely devoid of the long dark hairs that are abundant and conspicuous over particularly the upper half of this region in the worker; instead, there is a low, even, and rather plush-like growth of short, erect, silvery gray hairs, in abrupt contrast to the long black hairs that, as in the worker, crown the vertex. Unlike the condition in the worker, which has conspicuous erect hairs on the genal area, especially downward, the hairs on the genal area of the queen are very short although, like those of the worker, silvery gray. The lower margin of the clypeus fringed with stramineous to brownish hairs.

THORAX: With tessellation over most of its surface of the same dense and fine character as that of the worker; the tessellation is a trifle less dense on the mesopleura than it is on the mesonotum and scutellum and it is dense on the sides of the propodeum. In striking contrast to the condition in the worker there is a clearly demarked, hairless, large, V-shaped area at the base of the propodeum, which is highly polished and shiny, with scarcely a trace of sculpturing (fig. 70D). Thorax very much wider than that of the worker. The width of the mesonotum at the base about equal to the combined length of mesonotum and scutellum. The scutellum short, rounded posteriorly, not extended backward over the propodeum, which, contrary to the condition in the worker, is not so long in dorsal aspect as the scutellum.² Black with a dull yellow to reddish stripe, interrupted at the middle, on the posterior half of the pronotum and a maculation of approximately the same color rimming the posterior

² This, at least, is the condition in the specimen on which this description is based. Ducke, on the other hand, speaks of the propodeum as "descending very slantingly and hence long."

margin of the scutellum. Dense, appressed, short hairs of yellowish to brownish hue over the mesonotum and scutellum, giving these parts a sericeous sheen. In addition there are erect black hairs over the anterior part of the mesonotum and similar but still longer black hairs, backward-directed, on the scutellum, especially along or near the posterior margin. The erect hairs on the mesopleura grayish to brownish, short above but rapidly increasing in length downward, those on the lower half of the mesopleura and the under side of the thorax long and dense. Short, erect, dense, grayish hairs over the tessellated to here and there punctate sides of the propodeum.

LEGS: More robust than those of the worker, with the tessellation less uniform, more scattered and considerably lighter than on the head and thorax. The middle tibiae as well as the fore tibiae shorter than their respective femora; the hind tibiae barely if any shorter than the combined length of their femora and trochanters. The hind tibiae (fig. 70B) very different from those of the worker. Their outer face not in the least flattened but uniformly arched from base to apex except for sometimes a slight "dimple" on the posterior half at the apex. Their outline not in the least spoon-like, both the anterior and posterior lateral contours being approximately straight except for a slight convergence at the base, with the result that the joint is of rather uniform width over much of its extent; the apex bluntly angular. Hind metatarsi elongate; at their base, where they are widest, about one-half as wide as their tibiae but tapering towards the apex; their length about one-half that of their tibiae and approximating that of the small joints of the hind tarsi combined. Legs blackish (especially the femora and upward) to deep reddish brown (especially the tibiae and tarsi), with a faint yellowish maculation at the base of the outer face of each of the tibiae. The hairs abundant and on the whole rather long. They are silvery gray on the coxae and trochanters, and of like color but short and dense on the under side of the fore and middle femora. The under side of the hind femora, which has a deep, groove-like depression from the apex nearly to the base, has no hairs, but on the upper side of these femora there are a few hairs at the apex. The hairs on the tibiae and

tarsi (except for the light golden hairs that densely clothe the inner side of the several tarsal joints) are largely blackish. There are some erect hairs on the outer face of the fore and middle tibiae as well as along their anterior margin, but these hairs are fewer than those on the under side and fewer and shorter than those fringing the joint posteriorly. The longest hairs are on the hind tibiae, some of them being half as long or more than half as long as these tibiae are wide. They are numerous over the outer face of the joint and fringe it anteriorly and posteriorly and, while largely simple, here and there present feeble beginnings of a faintly branched condition. The gabled inner face of the hind tibiae with dark bristles on its short anterior slope and ridge, and with dense, appressed, sericeous hairs of slightly golden tinge on its longer posterior slope. The several metatarsi with dark hairs over their outer face; short dense reddish hairs along the anterior lateral margin of the middle and hind metatarsi and distinctly longer, strongly fringe-like, blackish hairs along the posterior lateral margin of all the metatarsi and along the anterior lateral margin of the fore metatarsi as well.

WINGS: Of about the same length as those of the worker but notably small when the larger body length and much more corpulent condition of the queen are taken into consideration, not or scarcely extending beyond the apex of the third abdominal tergite of the distended abdomen. Number of hamuli per lower wing eight. The transverse cubital veins obsolescent rather than obsolete, the first transverse cubital, at least, being clearly chitinized and demarked. The first discoidal cell about as 8 is to 9 compared with the length of the marginal cell. Wings subhyaline, slightly suffused with yellowish, their venation and stigma bright ferruginous.

ABDOMEN: Greatly distended, conspicuously wider than the thorax and about twice as long as the combined length of head and thorax. Coloration of abdomen, in contrast to that of the worker and male, reddish yellow, very closely approximating the predominant coloration of the abdomen in the worker of *quadripunctata* variety *bipartita*. The tergites rather uniformly tessellate to feebly punctate over most of their surface, and covered densely and evenly [except at

their bases of differentiated sculpture (in the virgin queen probably concealed)] with rather short, sericeous, brownish yellow to grayish hairs,¹ the coloration being somewhat dependent on the angle from which the hairs are viewed. The under side of the abdomen with an almost plush-like, dense, uniform growth of sericeous hairs of yellowish to gray coloration that covers virtually its entire surface. The sixth sternite with a small notch at its apical middle (fig. 70C).

MEASUREMENTS: Length 11 mm. (of which the abdomen occupies about 7.5 mm.); width of thorax about 3 mm.; length of forewing, including tegula, about 7 mm.

MALE

Hair usually predominantly pale over head, thorax, legs, and abdomen. Mesonotum usually without a lateral stripe. Abdomen black or fuscous.

HEAD (FIG. 67A): Black throughout except for the yellowish to cream-colored maculations on its lower half, which include: usually the entire clypeus except for a faint vestige of two embedded, parallel, longitudinal lines (see discussion), a triangle or subtriangle in the area between the clypeus and the inner rim of the eye and terminated about at the level of the base of the clypeus, a small supra-clypeal maculation (usually slightly emarginate below) that is wider than high. In most of the specimens the labrum is black or blackish with only the apical extremity touched with ferruginous (see discussion). The hairs much more extensively silvery gray than in the worker, only the vertex and the extreme upper part of front usually with at least a few dark hairs, the other hairs of the head being pale. The scape black. The flagellum sometimes a dull and rather uniform grayish black both below and above, in other

instances (a specimen from Petropolis, Brazil) bright ferruginous below, strongly contrasting with the dark scape.

THORAX: Black, but with usually the following areas yellow: a transverse stripe, medianly interrupted, across the posterior half of the pronotum; the axillae; and a half-circle bordering the posterior rim of the scutellum and briefly interrupted or narrowed at its middle. Usually no stripe bordering the mesonotum laterally. The hairs on the mesonotum and scutellum exclusively or almost exclusively silvery gray in contrast to those of the worker. The hairs on the mesopleura, on the thorax beneath, on the tegulae anteriorly, and on the propodeum likewise silvery gray.

LEGS: Blackish to brownish, rarely with a pale spot at the base of the tibiae. The hairs on the tibiae and tarsi silvery gray, as are those of the more basally located joints, only the metatarsal brushes sometimes a little more yellowish.

WINGS: Tinged approximately like those of worker. Number of hamuli in the 12 lower wings available for examination varied from seven to nine. Of these there was one that had seven hamuli, five that had eight hamuli, and six that had nine hamuli, an average of 8.42.

ABDOMEN: Black or fuscous, with the hairs not only of tergite 1 but of the subsequent tergites as well silvery gray, but black hairs tend to make their appearance towards the apex of the abdomen, and the hairs of at least tergite 7 and the hairs fringing the abdomen apico-laterally are dark brown to black. The hairs on the ventral surface of the abdomen silvery gray, those of the conspicuous fimbria of sternite 3 sometimes a little yellowish or even fuscous viewed from in front. (Fig. 69.)

MEASUREMENTS: Length 5.5 to 7.5 mm.; width of thorax 2.25 to 2.5 mm.; length of forewing, including tegula, about 7 mm.

TYPE MATERIAL

Two specimens in the Muséum d'Histoire Naturelle in Paris have been designated as the type of *quadripunctata*. On one of these the label reads "Brésil, Les Missiones," on the other the locality designation is "Cie de Rio Grande." As *quadripunctata* was described from "Capitainerie de Goyan,"

¹ Rather at variance with this description is the condition noted by Ducke (1925, pp. 425-426) in the case of the queen of *quadripunctata* that he described. Of the queen Ducke said: "Abdomen on the basal part shiny, with scattered coarse punctures, but on the apical part only slightly shiny, with denser and finer punctation, above and below with scant short rust-colored hairs."

In this connection mention may be made that Holmberg, too, had before him a queen of *quadripunctata*, regarding which he commented that it "differs a little from the description of the worker."

neither of these specimens can be part of the authentic type material, but they accord with what has been interpreted to be *quadripunctata*.

Doubts may still be raised, however, whether *quadripunctata* as described by Lepeletier was not an insect different from the interpretation that has been given it. Strengthening these doubts is the fact that, while *quadripunctata* is no. 27 in Lepeletier's list, no. 31 is the variety *bipartita*. Yet, though *bipartita* is structurally identical with *quadripunctata*, as generally interpreted, no comparison is drawn by Lepeletier between the two; instead, *quadripunctata* is said to have the stature of *vidua*, an Old World stingless bee, while *bipartita* is stated to resemble *ruficrus* in size (Lepeletier, 1836, pp. 430, 432-433).

DISCUSSION

Lepeletier's type of *quadripunctata* (a worker) had a clypeus with "a yellow maculation ending in three short points." Even among the few specimens of the worker of *quadripunctata* before me there is considerable diversity in the maculation of the clypeus and the parts adjacent to it. In specimens from Nova Teutonia, in the State of Santa Catharina, and in specimens from Jundiáhy and São Paulo, in the State of São Paulo, and in specimen A from Passa Anatro, Brazil, the maculation has the form of a massive inverted T. This is the condition, too, in a specimen from Bompland, Territory of Misiones, Argentina. In specimen B from Passa Anatro, Brazil, the clypeus is largely reddish black, with a longitudinal line of pale yellow traversing the dark area medianly. In contrast, specimen C with identical locality label has the clypeus wholly bright yellow except for two parallel, embedded, longitudinal, dark, abbreviated stripes. There is in all of the specimens a subtriangular yellow maculation at each side of the clypeus in the space between the clypeus and the inner orbit of the eye and terminating at or before the base of the clypeus. The small supraclypeal maculation, rarely extending upward beyond the antennal sockets, is somewhat wider than long and usually emarginate below and flat or slightly emarginate above. The labrum is black or largely black in specimens from

Jundiáhy, São Paulo, and Passa Anatro, and in some of the specimens from Nova Teutonia; in contrast, the labrum of two specimens from Ilha Secca is an almost unclouded yellow.

The facial maculations of the male of *quadripunctata* are a near duplication of those of the worker except that the clypeus is more apt to be completely maculated, with only a faint survival of embedded dark lines, even such vestige having sometimes faded out. One of the specimens, however, bearing the same data on the label as other specimens of full maculation, has the clypeus much invaded by black, and it is to be assumed, therefore, that in the case of the male as in the case of the worker the maculation of the clypeus is subject to variation. While most of the males have the labrum blackish, in two instances the labrum is ferruginous to yellowish, and one of the specimens thus distinguished (from Santa Catharina) has also the mandibles yellowish at the base and ferruginous at the apex. Certain males without locality designation, labeled merely 84-16, have maculations more nearly cream colored than yellow, and one of them lacks the transverse stripe on the pronotum. On the other hand, a second specimen has a faint trace of a stripe along the lateral borders of the mesonotum, which is an approximation to the condition of the males of variety *bipartita* before me. Possibly the exclusively black mesonotum of *quadripunctata*, characteristic of the workers before me, is shared to only a limited extent by the males. The small number of males available for study makes for caution in arriving at a conclusion.

Hermann von Ihering (1903, pp. 227-228) described two nests of *quadripunctata*, both of which were located in the earth, one at a depth of 3 meters, the other at "a considerable depth." The first nest measured 14 cm. by 10 cm., the second one 21 cm. by 15 cm., although the former consisted of eight combs as against seven in the latter. The arrangement of the combs was spiral, but the individual combs were connected at intervals by short wax pillars. The shape of the nest von Ihering described as that of "a baking oven or a half of an orange." The arched upper surface consisted entirely of a dense network of fine wax lamellae, in the numerous wind-

ing and ramifying passageways of which the worker bees lingered during periods of rest. The flat base consisted of a hard, thicker, and very fragile dark brown plate. The diameter of the entrance tube was in the two nests, respectively, 17 mm. and 10 mm. The oval-shaped honey and pollen pots of the first nest were 30 mm. high by 20 mm. wide, those of the second nest, which were located not below the combs but laterally along the rim, forming almost a ring, were 40 mm. high by 22–30 mm. wide. In contrast the brood cells measured only 5 mm. in height by 4 mm. in width.

From Paraguay, Fiebrig reported a nest of *quadripunctata* that was located at the terminus of a perpendicular subterranean passageway 80 cm. deep in sandy soil. The nest occupied a hollow about 30 cm. in diameter (cited by Strand, 1909, p. 235).

Bertoni (1911, p. 142), who reported *quadripunctata* as not uncommon at Puerto Bertoni, Paraguay, also indicated that the nests are subterranean, although the depth at which he stated they are generally found, 30 to 50 cm., is far less than that indicated for at least one of the nests noted by von Ihering and for the nest reported by Fiebrig. Bertoni stated that the nest entrance is devoid of a protruding tube or trumpet, but Ducke (1925, p. 426) and Bischoff (1927, p. 293) were of the opinion that the nests of *quadripunctata*, although subterranean, might have an earthen extension of the entrance above the level of the ground, possibly based on the fact that a very short protruding tube has been reported for the closely related *bipartita* or *basalis* (H. von Ihering, 1903, p. 205; Marianno, 1911, p. 80), which Ducke (1916, p. 139; 1925, p. 424; 1945, p. 105) regarded merely as an aberration of *quadripunctata*.

What might at first glance seem a valid record of a different nest habit is that reported by Holmberg (1887, p. 258), who indicated that *quadripunctata* makes its nest in the hollow of trees. However, in this instance Holmberg seems to have been misled in associating *quadripunctata* with a bee popularly known as "mombuca" (possibly *capitata*), and he himself later retracted his identification (1887, p. 282). Hence his comments on the biology are negligible.

According to Bertoni (1911, p. 142) the

name in Guaraní for *quadripunctata* is "eira ihvihgwi," the meaning being "subterranean bee or honey." R. von Ihering (1940, pp. 62, 381, 406) listed as popular names for *quadripunctata* the following: "irussú mineiro," "guirussú," "guirussú mineiro," and "abelha mulata."

DISTRIBUTION

Lepeletier (1836, p. 430) described the species from Goyaz in Brazil, and Marianno (1911, pp. 123–124) recorded it also from that state. Ducke (1916, p. 141; 1925, p. 426; 1945, p. 106) included in the range of *quadripunctata* localities in the Brazilian States of Minas Gerais, Rio de Janeiro, São Paulo, and Paraná, but it is not clear whether these are all references to the typical variety or whether they include also the aberration *bipartita*. Strand (1909, p. 235; 1910, p. 559) reported *quadripunctata* from several localities in Paraguay, and Bertoni (1911, p. 142) stated that *quadripunctata* is "not rare" in Puerto Bertoni in that country. Holmberg (1887, pp. 280–281; 1903, p. 377) reported it from Misiones, Argentina.

The specimens before me are from the following localities:

BRAZIL: State of Minas Gerais: Lassance, Nov. 9–19, 1919 (Cornell Univ. Exped.). State of São Paulo: Jundiahy, Oct. 12, 1897 (Schrottky); São Paulo, July 27, 1899 (Ihering), and 1899 (Ihering); Ilha Secca, Dec., 1919 (Cornell Univ. Exped.). State of Santa Catharina: Males without locality designation; Nova Teutonia, Sept. 26, 1939 (F. Plaumann). There are also specimens from a Brazilian locality designated Passa Anatro.

ARGENTINA: Territory of Misiones: Bompland (F. and M. Edwards).

Trigona (Schwarziana) *quadripunctata* variety *bipartita* (Lepeletier)

Melipona (*Trigona*) *bipartita* LEPELETIER, 1836, pp. 432–433.

Trigona bipartita, F. SMITH, 1854, p. 408.

Trigona basalis F. SMITH, 1854, p. 412.

Trigona basalis, F. SMITH, 1866, pp. 326–327.

Trigona basalis, F. SMITH, 1868, p. 134.

Melipona basalis, PECKOLT, 1893, p. 580.

Melona [sic] *basalis*, PECKOLT, 1894, p. 90.

Melipona basalis, DALLA TORRE, 1896, p. 576.

Trigona basalis, H. VON IHERING, 1903, pp. 205, 237, 240.

Trigona basalis, GRÜNBERG, 1904, p. 9.

Trigona quadripunctata, H. VON IHERING, 1904b, p. 386.

Trigona bipartita, COCKERELL, 1905, p. 323.

Trigona bipartita, DUCKE, 1910b, p. 368.

Trigona basalis, MARIANNO, 1911, pp. 40, 80-81.

Trigona bipartita, MARIANNO, 1911, p. 82.

Trigona quadripunctata aberration *bipartita*, DUCKE, 1916, pp. 139-141.

Trigona quadripunctata aberration *bipartita*, DUCKE, 1925, pp. 424-426.

Melipona quadripunctata aberration *bipartita*, ALFKEN, 1930b, p. 10.

Melipona quadripunctata aberration *bipartita*, ALFKEN, 1932b, p. 306.

Trigona basalis, SCHWARZ, 1932a, p. 259.

Trigona bipartita, SCHWARZ, 1932a, p. 259.

Trigona quadripunctata, MAIDL, 1934, p. 575.

Trigona (Schwarziana) quadripunctata bipartita, MOURE, 1944b, p. 2.

Melipona quadripunctata aberration *bipartita*, DUCKE, 1945, pp. 105-107.

WORKER

DIAGNOSTIC CHARACTERS: Like typical *quadripunctata* structurally but with the tergites of the abdomen either wholly reddish yellow (*bipartita*) or with the basal tergite black and tergites 2 to 6 reddish yellow (*basalis* Smith), which is the more usual condition.

HEAD: Black throughout except for the maculations that are confined to the lower half of the face, and these exceedingly variable both in extent and in clarity even in a series from a single locality (see discussion). The maculation on the clypeus frequently of the shape of an inverted T, but sometimes the clypeus is largely black and in other cases predominantly yellow. The side-facial maculations, occupying the triangle between the clypeus and the inner orbit of the eye and terminated at or before the base of the clypeus, vary, as does the clypeus and usually in conformity with it, from bright pale yellow to dull brownish. The supraclypeal maculation, like that of typical *quadripunctata*, wider than high and often emarginate below, variable in the intensity of its coloration to about the same extent as the clypeal and side-facial maculations. Labrum usually black, rarely yellow. Mandibles variable from mostly yellow to reddish, or reddish apically and black basally. The coloration of the hairs somewhat variable; on the whole the black

hairs not so predominant as in typical *quadripunctata*. Black are the hairs on the vertex and upper part of front. The hairs on clypeus sometimes of intermixed character, black and silvery gray, but in other cases wholly silvery gray. The hairs fringing the mandibles below ferruginous to brownish. The other hairs of head, including those of the genal area and lower part of front, silvery-gray. Scape black; flagellum black above, ferruginous below.

THORAX: Black, with the maculations and coloration of the hairs usually as described for typical *quadripunctata*, although in the type specimen of *bipartita* the maculation on the axillae has faded out.

LEGS: Brownish to blackish, with the hairs as in typical *quadripunctata*.

WINGS: Like those of typical *quadripunctata*. Number of hamuli per lower wing ranges from seven to 10. Of 56 wings examined, I found only one wing that had as few as seven hamuli and only one that had as many as 10 hamuli. There were 29 of the total that had eight hamuli and 25 that had nine hamuli, an average for the 56 wings of 8.46.

ABDOMEN: Differs emphatically in its coloration from typical *quadripunctata* in having tergites 2 to 6 not black but usually entirely reddish yellow. Tergite 1 may be reddish yellow but is more often black or fuscous. The sternites, like those of typical *quadripunctata*, black. The hairs silvery gray on tergite 1 and on the under side of the abdomen (with the exception sometimes of the last visible sternite, the hairs of which may be black). There are apt to be short silvery gray hairs, too, on tergites 2 to 6, but the relatively long hairs on tergite 6 and some of the hairs also on tergites 4 and 5 tend to be black.

MEASUREMENTS: Length 5 to 6.5 mm.; width of thorax 2.25 to 2.5 mm.; length of forewing, including tegula, 6.25 to about 7 mm.

QUEEN

Unknown.

MALE

Hair predominantly silvery gray on head, thorax, legs, and abdomen. Mesonotum usually with a lateral stripe. Abdomen with the middle part of the tergites more or less ex-

tensively black but the lateral extremities reddish yellow (callow condition?) and the apical rims also as a rule at least a cloudy reddish or yellowish.

HEAD: Black throughout except for the following yellowish to cream-colored area on its lower half: the clypeus, a triangle at each side of the clypeus in the space between the clypeus and the inner orbit of the eye and terminated at about the base of the clypeus, and a small supraclypeal maculation (usually slightly emarginate below) that is wider than high. The labrum ferruginous or sometimes black. The mandibles black basally but with their apex more or less extensively ferruginous. The scape sometimes entirely black, at other times with a more or less developed stripe anteriorly; the flagellum with joint 1 black and sometimes also joint 2, the subsequent joints grayish black above but reddish below although the apical half of the apical joint is apt to be black both below and above. The hair almost exclusively silvery gray, with only feeble admixture at most of dark hairs on the vertex.

THORAX: Black with the following pale yellowish to ferruginous maculations: a medianly interrupted transverse stripe across the posterior half of the pronotum, a stripe along each side of the mesonotum, a maculation on the axillae, a semicircle (more or less interrupted at the middle) encircling the posterior rim of the scutellum, and sometimes a transverse stripe just beyond and below the scutellum. The hair of the thorax somewhat variable: in specimens from Rio de Janeiro silvery gray on mesonotum and scutellum, in specimens from Petropolis silvery gray intermixed with black to mainly black. The mesopleura, on the thorax beneath tegulae anteriorly, and propodeum with silvery gray hairs.

LEGS: Blackish, more or less streaked and spotted with ferruginous, there being as a rule more or less vague stripes on the femora beneath of the middle and hind legs, suffusions of ferruginous on some or all of the tibiae within, at the apex of the femora, at the base and more particularly at the apex of the fore and middle tibiae externally, and usually the tarsal joints are entirely or predominantly ferruginous. The hairs of the leg somewhat variable: in all cases predomi-

nantly silvery gray, in the specimens from Rio de Janeiro virtually entirely so, in the specimens from Petropolis with some admixture of darker hairs, particularly on the outer face of the hind tibiae.

WINGS: Approximately as in typical *quadripunctata*. Number of hamuli per lower wing range from seven to nine, with only one specimen having either as few as seven or as many as nine hamuli, and six specimens having eight hamuli. The average per lower wing in the 16 wings examined was eight hamuli.

ABDOMEN: In contrast to the usual condition of the worker, with considerable black on the dorsal middle of each tergite, but all of the tergites (even the usually more extensively black tergite 1) flanked on each side with reddish yellow, and the apex of the tergites frequently more or less cloudy reddish or reddish yellow with, in some cases, even a narrow yellowish fragmentary band. The under side of the abdomen reddish yellow to brownish, more or less stained with blackish, and with the hairless basal part of sternite 3, which bears the conspicuous fimbria medianly, definitely dark. The hairs not only of tergite 1 but of the subsequent tergites as well silvery gray, but black hairs tend to make their appearance towards the apex of the abdomen, and the hairs of at least tergite 7 and those fringing the abdomen apico-laterally are dark brown to black. The hairs on the under side of the abdomen silvery gray for the most part, those of the conspicuous fimbria on sternite 3 rather yellowish with some dark hairs, and the forward-pointing hairs of sternite 4 distinctly dark in at least the specimens from Petropolis.

MEASUREMENTS: Length 5.5 to 7.5 mm.; width of thorax 2.25 to 2.5 mm.; length of forewing, including tegula, about 7 mm.

TYPE MATERIAL

Described from Brazil. The type is in the Muséum d'Histoire Naturelle in Paris. The type of *basalis* is in the British Museum.

DISCUSSION

The maculations of the face are in the worker of *bipartita* rather variable. F. Smith's *basalis*, which is usually considered a synonym of *bipartita*, has merely a yellow per-

pendicular line down the middle of the clypeus, whereas the type of *bipartita* has a clypeus that is largely yellow. Indeed the maculation of the clypeus of *bipartita* shows a range even greater than that noted for typical *quadripunctata*, although this conclusion is very likely due to the more ample material of *bipartita* and the less abundant material of typical *quadripunctata* before me. A specimen from Bello Horizonte, for instance, has the clypeus almost completely vivid yellow with merely a trace of embedded black lines, and this condition is approximated in one of the four specimens from Lassance, the other three specimens from that locality being progressively darker, with merely a longitudinal median stripe of yellow bisecting a dark area in the case of one of them, a condition paralleling *basalis*. All of the specimens in a large series from Petropolis have the clypeal maculation, as indeed the other maculations, subdued and diluted, but whereas in some of these the maculation of the clypeus is of the usual inverted T shape, in others the black has so encroached on the maculation as to leave only fragmentary and semi-extinguished remnants of the inverted T. In such cases the side-facial and supra-clypeal maculations are usually so subdued as to be traceable only as a brownish discoloration. The specimen from Bello Horizonte is exceptional in having a bright yellow labrum and largely yellowish mandible, resembling in these respects the specimens from Ilha Secca discussed under typical *quadripunctata*. Two of the specimens from Lassance also have the mandible mainly yellowish, but in the other two specimens the hue is reddish. In the specimens from Rio de Janeiro the apical region of the mandible is reddish, but the basal region is black to a variable extent and sometimes over most of the mandible. This, too, is the condition in the series from Petropolis.

In respect to the maculation of the thorax the type of *bipartita* is exceptional in lacking spots on the axillae and in having merely a faded maculation rimming the posterior edge of the scutellum. This maculation is very faded, too, in some of the specimens from Petropolis.

The name *basalis* was conferred by F. Smith presumably because of the contrasting

dark basal tergite of the abdomen, all of the other tergites being usually reddish yellow in the worker. On the other hand, the type of *bipartita*, in conformity with the description of that insect, has not merely tergites 2 to 6 but also tergite 1 reddish yellow. The condition represented in the type of *basalis* is the far more usual one, but even among the few specimens before me from Lassance both conditions are represented.

It is of interest that, although the worker of *bipartita* has the tergites of the abdomen beyond tergite 1 as a rule exclusively reddish yellow and the sternites black, in the few males before me this condition is reversed, the tergites being in all cases more or less invaded by black, especially medianly, and the sternites, by way of compensation, having considerable reddish or brown. This, too, was the condition of the males from Cantagallo,¹ southern Brazil, to which Smith (1866, pp. 326-327) refers. The darkening of the upper surface of the abdomen, in some of the specimens very extensive, represents an interesting approximation in the male of *bipartita* to the condition of typical *quadripunctata*. Indeed it is possible that the specimens thus characterized are callows and that the mature male has an abdomen even more completely black, at least above.

Smith (1866, pp. 326-327) stated that his males from Cantagallo had the clypeus "pale testaceous, nearly white." In the specimens before me the coloration is pale yellowish and, unlike the males of typical *quadripunctata*, all traces of embedded dark lines in the clypeus are wanting. Reversing the condition noted for typical *quadripunctata*, only one male of *bipartita* has the labrum black. On the other hand, all of the males of *bipartita* before me have the mandible black with merely the apex ferruginous, although the number is too limited to rule out the belief that *bipartita* males, like the exceptional *quadripunctata* male, may not sometimes have the mandible basally yellow. A condition at variance with the males of typical *quadripunctata* is the red under surface of the flagellum and the presence in two of the males

¹ This locality is spelled Catagallo in F. Smith's paper of 1866, but the correct spelling appears in his paper of 1868 (p. 133).

of *bipartita* (from Rio de Janeiro) of a stripe on the scape in front.

It is a surprise to find both in the males from Rio de Janeiro and from Petropolis a stripe along the side of the mesonotum, a condition at variance with that of the worker and one also probably rarely shared by males of typical *quadripunctata*. Smith (1866, pp. 326-327) does not mention such a stripe in his male specimens from Cantagallo.

The legs of the males described are very irregularly spotted with yellow, and part of this may be due to a more or less callow condition—it is difficult to say. Even Smith's male specimens, however, had the "articulations of the legs" ferruginous.

As does typical *quadripunctata*, the variety *bipartita* establishes its nest in the ground. Thus three-quarters of a century ago Smith (1868, p. 134) stated that it had the name of "earth-bee" because it makes its nest below the surface. A nest reported by H. von Ihering (1903, p. 205) was at a depth of 75 cm. Marianno (1911, p. 81) gave the range of depth as variable from scarcely 60 cm. to 1.2 meters, which, though an impressive achievement in excavation, falls far short of the maximum penetration of the earth (3 meters) reported for typical *quadripunctata* (H. von Ihering, 1903, p. 227). Although the nest of *bipartita* reported by von Ihering terminated in a simple flight hole, inhabitants of the region where it was found (Petropolis, Brazil) indicated that occasionally this bee prolongs the flight hole outwardly. This external prolongation Marianno (1911, p. 80) referred to as negligible (1 to 1.5 cm. with a diameter of 8 to 10 mm.). Marianno came to the conclusion that *bipartita* used abandoned formicaries of *Atta sexdens*. At Estação do Pilar he found six nests of *bipartita* within an area of 15 square meters that had formerly been occupied by an enormous nest of this ant. This conclusion is of interest, for Weyrauch has found that *Trigona* (*Paratrigona*) *lineata* variety *nuda* Schwarz occupies the fungus chambers of this ant in Peru.

Peckolt early proclaimed (1894, p. 90) the fact that this subgenus builds its nests only in the ground. His observations were made on the variety *bipartita*, and he had watched a nest from the surface for five years before finally yielding to the temptation of exca-

vating it. What was revealed when the nest was finally dug out is so at variance with other nests described that it is hard to interpret it. The nest consisted of four round balls of a firm earthen material, the first as large as a human skull, the others progressively smaller, the smallest being no larger than the skull of a small child. The first was at a distance of 40 cm. from the surface, the last at a depth of 1.32 meters. Because of the extraordinary nature of the structures, Peckolt drew the conclusion that from a parental nest three successive annual swarms had gone forth and established themselves in propinquity to the parental nest.

In Bahia *bipartita* was probably a visitor of one of the common Compositae with violet bloom (Alfken, 1930b, p. 10).

The honey was pronounced rather tasty by Marianno (1911, p. 81). He also spoke of it as scant, although the nests were "very populous."

According to both H. von Ihering and Marianno, the bees are very timid, and Marianno added that they are indolent (perhaps only seemingly so, for von Ihering explained that they do not fly to and fro as long as one remains in the vicinity of the nest).

It is interesting to learn through H. von Ihering that this bee is domesticated, being kept in boxes, and under such conditions soon loses its timidity, which would seem to be associated with a subterranean habit.

The name Peckolt (1893, p. 580) gave for this bee is "mombuco mirim," which differs sharply from the names applied to the closely related *quadripunctata* as recorded by Ducke (1925, p. 344). These are listed as "abelha mulata," "irussú mineiro," "irussú do chão," "guirussú." Two of Ducke's designations correspond, except for spelling, with those set down by H. von Ihering (1904b, p. 386) in his paper dealing with the Tupi (or perhaps more strictly Guaraní) origin of the names for certain species of Brazilian Meliponidae. The native names von Ihering gave for *quadripunctata* are "guiraçu" and "iraçu minerá."

DISTRIBUTION

Lepelletier (1836, pp. 432-433) described *bipartita* from Brazil, without more specific locality reference. F. Smith (1854, p. 412) recorded *basalis*, here considered a synonym

of *bipartita*, from both Brazil and Colombia, but the reference to the latter country would seem probably to be based on error. Not only are there no specimens before me from the northern half of South America, but the only other records of which I have knowledge all place the range southward in that continent. F. Smith himself had males from Cantagallo, in "southern Brazil" (1866, pp. 326-327), which is probably the Cantagallo in the State of Rio de Janeiro, although the number of localities in Brazil that bear this designation is bewildering and makes any selection of doubtful accuracy. Marianno (1922, p. 82), in his brief reference to *bipartita*, merely repeated Lepeletier's designation "Brazil" with the addition of a question mark, but the fact that Marianno made independent mention in his paper also of *basalis* (pp. 80-81) tends to indicate that he was probably not aware of the true nature of *bipartita*. Ducke (1916, p. 141; 1925, p. 426; 1945, p. 106) included in the range of *quadripunctata* localities in the Brazilian States of Minas Gerais, Rio de Janeiro, São Paulo, and Paraná. Very likely he intended to imply that the range of *bipartita*, which he lists as an aberration, coincides with that of typical *quadripunctata*, although this is not clear beyond question. That *bipartita* extends at least into the southern part of the State of Bahia is clear from the interesting record made by Alfken (1930b, p. 10), who reported that Roman took a specimen of *bipartita* at Iguassú. This is not the Iguassú located in the State of Rio de Janeiro but, as Roman explained (Alfken, 1930b, p. 2), a landed estate almost 300 kilometers westward of the city of Bahia or São Salvador.

The specimens of *bipartita* before me come from the following localities:

BRAZIL: State of Rio de Janeiro: Rio de Janeiro, 1897 (Peckolt), and 1901, including males; Petropolis, including males. State of Minas Gerais: Bello Horizonte, Nov. 1-8, 1919 (R. G. Harris, of Cornell Univ. Exped.); Lassance, Nov. 9-19, 1919 (R. G. Harris, of Cornell Univ. Exped.).

TRIGONA SUBGENUS PARAPARTAMONA,
NEW SUBGENUS

TYPE SPECIES: *Trigona zonata* F. Smith.

WORKER

DIAGNOSTIC CHARACTERS: Very finely tessellated, and rather densely so, especially on

the thorax; hind tibiae shaped much like the bowl of a spoon; wings conspicuously long. The sides of the face maculated strongly with yellow but the clypeus without or virtually without maculation.

HEAD (FIG. 71A): Somewhat wider than long, in the proportion of about 11 to 9. The facial quadrangle a little longer than wide, the distance from the middle ocellus to the apex of the clypeus being about as 8.5 is to 7 when compared with the distance between the compound eyes at the level just below the middle ocellus. The eyes at this level no farther or only barely farther apart than they are towards their lower extremity. The clypeus and supraclypeus both raised well above the sides of the face. The clypeus about three-fifths as long as it is wide, its apico-lateral extremities very remote from the eye and only slightly prolonged; its apex truncate along the middle, receding sharply towards the eye at each of its extremities; its surface somewhat arched. The mandibles (fig. 71A) overlapping, widest at apex and base, slightly narrowed towards the middle; the outer two-thirds of their apex edentate, the inner one-third with two well-defined denticles. Malar space very long, about as long as the mandible is wide at the base, and only a very little shorter at the inner extremity than at the outer. The labrum simple. The supraclypeus longer than wide, its somewhat pointed summit connected by a shallow fossa with the anterior ocellus. The middle ocellus a little anterior to the lateral ocelli, which are a little more prominent than the middle ocellus because they are raised and tilted each towards the nearest compound eye. The distance between the lateral ocelli less than that which separates each lateral ocellus from the nearest compound eye. The region behind the ocelli barely raised. The head very finely tessellated (almost approaching the smooth on the sides of the face), with the tessellation on the genal area about as dense and as delicate as that on the front and clypeus. Head black with yellow maculations. Clypeus dark, sharply contrasting with the strongly yellow side-facial maculations, a small supraclypeal maculation, likewise yellow, and the usually yellow, or largely yellow but sometimes ferruginous, labrum and mandibles. No, or only very short, erect bristles on the clypeus or sides of face, usually merely silvery gray ap-

pressed tomentum, but erect bristles are present in the supraclypeal area and extend thence over the front to attain their maximum length on the vertex. The hairs on the scape of variable length. Fairly long erect hairs on the lower one-third of the genal area, on the labrum, and on the inferior margin of the mandibles. The upper two-thirds of the genal area silvery gray pruinose. The scape somewhat more slender than the flagellum and about one-half as long.

THORAX: Black, immaculate, densely if finely tessellated; the propodeum of very pronounced length. The mesonotum is somewhat shorter than it is wide (about as 6 is to 7) and is less than twice as long as the dorsal face of the propodeum, which is much more lightly tessellated and hence more shiny than the densely tessellated mesonotum and mesopleura. The posterior face of the propodeum somewhat abruptly declivitous but not truncate. A deep fossa separates the posteriorly rounded and not extended scutellum, which is rather lightly tessellated and correspondingly shiny, from the mesonotum. The scutellum only about one-half as long as the propodeum. The mesonotum with a sericeous sheen but devoid or almost devoid of erect hairs, only a few inconspicuous short hairs of that type being detectable in contrast to the condition of the scutellum on which the hairs are more numerous and long. The mesopleura silvery gray pruinose and, in addition, with erect hairs. Erect hairs also on the sides of the propodeum as well as silvery gray appressed hairs. Appressed hairs are present also, although a little less densely, on the dorsal face of the propodeum. The mesonotum and the mesopleura immaculate.

LEGS: With very fine and feeble tessellation on the outer face of the fore and middle tibiae and with traces of sculpturing here and there on the other joints, but on the whole of smooth surface. The middle leg intermediate in length between the short fore leg and the long hind leg, which is about as long as the combined length of the head, thorax, and abdomen. The tibiae of the fore legs shorter than their femora, those of the middle legs about the same length as their femora, those of the hind legs somewhat longer than the hind femora plus trochanters. The hind tibia are a little more than one-third as wide as they are long, shaped much like the bowl

of a spoon, very deeply concave from close to the base to the apex (fig. 71B); the apical contour has a small angulation anteriorly, followed in turn by a convexity and an emargination, the latter terminating in a tooth where it meets the posterior lateral contour. The hind metatarsi about one-half the maximum width of the hind tibiae, rather parallel sided, narrowed a very little towards the base. The hairs on the coxae, particularly the hind coxae anteriorly, and under side of trochanters fairly long; those of the upper side of the fore and middle femora short, but hairs on under side of these joints longer. The hairs on outer face of the fore tibiae short but not quite so short as those on the outer face of the middle tibiae; the hairs that fringe the fore tibiae longer, nearly as long as those on the under side of the middle tibiae. The upper side of the hind femora with rather short hairs that are nevertheless longer than the exceedingly dwarfed hairs on the under side. The hind tibiae fringed anteriorly and posteriorly with eyelash-like hairs that, like the other hairs of the leg, are simple. The inner face of the hind tibiae unevenly gabled, with semi-erect hairs along the ridge and microscopic appressed hairs rather densely covering the posterior slope, which is the longer of the two sloping surfaces that form the gable. The hairs long on the outer face of the front metatarsi, shorter on the outer face of the middle and hind metatarsi except that near the anterior contour of the hind metatarsi there are some rather long hairs.

WINGS: Very long in comparison to the body. The first discoidal cell only about two-thirds as long as the marginal. The transverse cubital veins indicated with some clarity, obsolescent rather than obsolete. Number of hamuli per lower wing in the specimens before me only five.

ABDOMEN: Comparable in width with the thorax, of generally oval contour viewed from above; its segments tending to be rather fully exposed instead of telescoped; densely if finely tessellated, with a dull sheen. Sometimes a very few inconspicuous hairs on each side of the basin-like depression on tergite 1. The dorsal aspect of segments 1 to 5 without, or with only a few, sporadic semi-erect hairs, these tergites usually having merely an inconspicuous covering of microscopic, ap-

pressed, pale hairs. Tergite 6 with semi-erect hairs that are relatively long and readily noted. Erect hairs are present somewhat sparsely on all the sternites, especially down their middle, in addition to much more abundant silvery gray appressed hairs.

MEASUREMENTS: Length 5 to 6.5 mm.; width of thorax about 2.25 mm.; length of forewing, including tegula, about 7.75 to 8.5.

QUEEN

Unknown.

MALE

Unknown.

DISCUSSION

This subgenus, confined to *zonata* and the varieties of *zonata*, is of unusual appearance. Very delicately tessellated (much more finely so than are, for instance, members of the subgenera *Schwarziana*, *Paratrigona*, and *Cephalotrigona*), it occupies a position somewhat intermediate between the subgenera of smooth and those of roughened exoskeleton. It combines with this, in itself, interesting condition the large spoon-shaped or bowl-shaped hind tibiae of members of the subgenus *Partamona*. The unusually long propodeum, the dorsal aspect of which is only slightly less than twice the length of the scutellum, is another striking character. Finally the maculations arrest one's interest: the strongly yellow, upward tapering stripes along the sides of the face to nearly the level of the anterior ocellus, flanking an immaculate clypeus, with a small, somewhat trapezium-shaped yellow spot in the supraclypeal area, and the usually yellow coloration of the labrum and mandibles.

Notwithstanding its conspicuously long wings, *Parapartamona* has few hamuli, regularly five in the small aggregate of specimens before me. This is one of the indications that, notwithstanding its sculpturing, *Parapartamona* is probably rather removed from the borderland where *Melipona* and *Trigona* tend to meet. The subgenus *Partamona* would seem to be its closest relative, but male specimens are desirable for a further clarification of the group.

Nothing, unfortunately, is known regarding the biology of this rare subgenus.

KEY TO THE VARIETIES OF *Trigona* (*Parapartamona*)

WORKERS

1. The tergites of the abdomen deep reddish brown with an ill-defined banding of black along the apex of each. The eyelash-like hairs fringing the hind tibiae anteriorly and posteriorly ferruginous
 *zonata* variety *caliensis*, new variety
 The tergites of the abdomen with at least some flavous, often predominantly flavous . . . 2
2. The bristles on the scape short, no longer than the scape is wide, and largely pale. The eyelash-like hairs fringing the hind tibiae ferruginous. Tergites 2 to 5 with merely lateral flavous spots on an otherwise mainly dark surface, no continuous flavous bands . . .
 *zonata* variety *brevipilosa*, new variety
 The bristles at the base of the scape long, about twice as long as the scape is wide, and black. The eyelash-like hairs fringing the hind tibiae blackish. Tergites 2 to 5 with more or less distinct darker banding apically but with an area of flavous basad of these bands that extends unbroken from one lateral extremity to the other 3
3. The band along the apex of tergites 2 to 5 deep reddish black that contrasts with the flavous area. *zonata* variety *zonata* F. Smith
 The band along the apex of tergites 2 to 5 faintly roseate, blending with the flavous area.
 *zonata* variety *tungurahua*, new variety

Trigona (*Parapartamona*) *zonata* variety *zonata* F. Smith

Trigona zonata F. SMITH, 1854, p. 411.

? *Trigona alfkeni*, FRIESE, 1900a, p. 393.

? *Trigona alfkeni*, FRIESE, 1901, p. 266.

WORKER

DIAGNOSTIC CHARACTERS: The long bristles on inner side of scape and the eyelash-like hairs fringing the hind tibiae anteriorly and posteriorly are blackish. Tergites of abdomen bright yellow over most of their surface with a contrasting band of deep reddish black along the apex of each. The venter somewhat more sooty yellow with a narrow dark band on the apex of the several sternites.

HEAD: Black, slightly tinged with reddish on the clypeus. The labrum, the mandibles except for their teeth and black basal prominences, the antennal sockets and adjacent basal region of the scape in front, and the

flagellum below reddish. More conspicuous than the ferruginous maculations are, however, the following strongly yellow maculations: a small trapezium-shaped spot between the antennal sockets and a clavate maculation flanking the inner orbit of the eye to nearly the level of the anterior ocellus, broad below where it adjoins the clypeus and inflexing, rather abruptly narrowed near the level of the base of the antennae and thence continued upward tapering. No erect bristles on the clypeus or sides of the face, merely silvery gray, appressed tomentum, but erect black bristles are present in the supraclypeal area and extend thence, progressively longer, over the front to attain their maximum length on the vertex. The black bristles on inner side of scape unusually long though few, some nearly twice as long as the scape is wide. There are hairs of lighter hue, ferruginous to copper colored, along the lower one-third of the genal area, on the labrum, and fringing the inferior margin of the mandibles. The upper two-thirds of the genal area is covered with pale tomentum like that on the clypeus and sides of face, and not much more densely.

THORAX: Black, immaculate. The mesopleura silvery gray pruinose and with erect silvery gray to ferruginous hairs, this intermingled growth extending in even greater density to the areas on each side of the propodeum; silvery gray appressed hairs are more sparsely present over the dorsal face of the propodeum. There are a few erect long black hairs on the scutellum, especially posteriorly.

LEGS: Blackish, the small tarsal joints of all the legs as well as the metatarsus of the fore legs brownish. The hairs on the coxae and under side of trochanters pale; those of the femora darkish on the upper face of the joint and pale on the under face of the joint. The hairs on the under side of the fore and middle tibiae pale. The eyelash-like hairs fringing the anterior and posterior contours of the hind tibiae dark. The brushes on the inner face of the metatarsi golden to copper colored.

WINGS: Lutescent, with the median cell distinctly yellowish. The venation ferruginous, the stigma brightly so. The tegulae deep reddish.

ABDOMEN: Tergites 1 to 5 bright yellow over most of their surface with a contrasting band of deep reddish black along the apex of each. The dark band on tergite 1 is terraced, with a narrow upper element resting on the broader base of the lower one. The dark bands on tergites 2 to 5 are broadest at the middle and taper towards each side. The usually concealed extreme base of each tergite gives evidence of a narrow basal border of black. The ventral aspect a little more sooty yellow, with the dark bands on the apex of the sternites narrower than those on the tergites. The erect hairs down the middle of the sternites brownish with, in addition, inconspicuous, pale, appressed hairs on each side of the sternites.

MEASUREMENTS: Length 6.5 mm.; width of thorax about 2.25 mm.; length of forewing, including tegula, about 7.75 mm.

QUEEN

Unknown.

MALE

Unknown.

TYPE MATERIAL

What is presumably the type, or at least part of the type material, is in the W. Saunders collection at Oxford University. It was collected at a locality, the name of which is not clearly decipherable, in Colombia (see distribution, below).

DISCUSSION

The species *zonata* has been largely neglected in the literature, probably because it is a very rare insect. In the collections before me there are scarcely more than a half dozen examples and yet, because they come from different localities and have rather distinct characters, I have been impelled to recognize several varieties among them. The typical variety is readily known by the summary of its more distinctive characters given at the beginning of the description offered in this paper.

It seems not unlikely that Friese's *alfkeni* is close to, or identical with, typical *zonata* (see discussion of *zonata* variety *caliensis*, p. 437).

Typical *zonata* is approximated by the variety *tungurahuana*.

DISTRIBUTION

Frederick Smith (1854, p. 411) described *zonata* from Colombia without more specific locality reference. The specimen that is here interpreted as the type bears one label reading Col. and a second label, almost undecipherable but, as nearly as I can interpret it, spelling "Paramo Lutagnetugao," a place I have been unable to locate in any atlas. On the following line of the same label appear the words "Cordillera VI." On the under side of this label appears "*Trig. Bogotaensis*," probably a tentative name for what Smith later decided to call *zonata*. A paramo seems curiously out of accord with the usual habitat of stingless bees, but the suggestion of treelessness is interesting in that it conjures up the possibility that *zonata*, like the members of the subgenus *Schwarziana* and some of the colonies of *Partamona*, is not arboreal but subterranean in its nest habits.

Trigona (Parapartamona) *zonata* variety
tungurahuana, new variety

WORKER

DIAGNOSTIC CHARACTERS: Structurally and in its sculpturing conforming with the description of the subgenus. The long bristles on the inner side of the scape as well as the eyelash-like hairs fringing the hind tibiae anteriorly and posteriorly are blackish as in the typical variety. The abdomen, in contrast to that of the other varieties, an almost unsullied flavous both dorsally and ventrally, with a narrow dark stripe only at the base of tergite 2 and faded roseate bands apically on the subsequent tergites, but these bands so vague that in certain lights they all but blend completely with the basal flavous.

HEAD: Like that of the typical variety, black with the following parts bright flavous: the labrum; the mandibles except for their roseate apical half, blackish apical rim, and black basal prominences; a small trapezium-shaped maculation between the antennal sockets; a stripe along the inner orbit of the eye, clavate below at the level of the clypeus and in-facing, rather abruptly narrowed at the level of the antennal sockets, and ter-

minating somewhat below the level of the middle ocellus. A more fulvous stripe on the scape in front; the flagellum predominantly black with some of the joints briefly touched with fulvous at the apex of their under side and joint 2 more completely fulvous. Microscopic silvery gray appressed hairs over the clypeus and upper half of the head and, in addition, erect black hairs between the antennae, on the front, and on the vertex. The bristles on the scape likewise black, those on the inner side near the base about twice as long as the scape is wide. The genal area silvery gray pruinose, its lower part with concolorous erect hairs. The hairs fringing the inferior margin of the mandibles and those on the labrum ferruginous.

THORAX: Black, with the exception of the dull ferruginous tubercles. The entire surface of the mesonotum with a dark sericeous sheen and a few inconspicuous erect black bristles along its sides. The black bristles on the scutellum much longer, somewhat comparable in size with the length of the scutellum itself. The mesopleura silvery gray pruinose and, in addition, with erect ferruginous to slightly brownish hairs that increase in length and grade into silvery gray on the under side of the thorax, where the hairs approximate in length those of the scutellum. The silvery gray tomentum dense on the sides of the propodeum, where, in addition, there are erect hairs; the dorsal surface of the propodeum more lightly covered with silvery gray appressed hairs.

LEGS: Mainly black, with the trochanters beneath, the fore tibiae within, and the fore metatarsi and the succeeding small joints fulvous to ferruginous; the small joints of the middle and hind tarsi darker brownish; the hind femora beneath and the hind tibiae somewhat suffused with dark reddish brown. The hairs on the coxae, under side of trochanters, and under side of femora silvery gray, with the much shorter hairs on the upper side of femora darkish. The short semi-erect bristles on the outer face of the fore tibiae, the slightly shorter hairs of similar character on the corresponding face of the middle tibiae, and the eyelash-like hairs fringing the anterior and the posterior contours of the hind tibiae black; the hairs on the inner face of the fore tibiae and the longish hairs on

the inner face of the middle tibiae silvery gray to ferruginous. The long hairs on the outer face of the fore metatarsi and the shorter hairs on the subsequent tarsal joints also silvery gray to ferruginous; the fore metatarsal brush golden. The hairs on the external face of the tarsal joints of the middle and hind legs black, the metatarsal brushes somewhat variable in color according to the angle from which they are viewed, reddish golden in some lights, more silvery in others.

WINGS: Lutescent, with the median cell more distinctly yellowish. The venation and stigma ferruginous. The tegulae blackish, with a deep reddish, semitransparent pupil. Number of hamuli per lower wing five.

ABDOMEN: Almost completely flavous both dorsally and ventrally except for an abbreviated narrow blackish stripe at the base of tergite 2 (which gives the illusion that there is a dark fascia also on the overlying transparent apical rim of tergite 1) and a faint roseate band along the apex of tergites 2 to 5. The tergites covered somewhat densely with microscopic appressed hairs that, viewed from certain angles, give forth a silvery gray sheen but, viewed from above, appear dark against the flavous chitin. The tergites other than tergite 6, which has rather long black bristles, with only a few semi-erect black hairs. The sternites silvery gray sericeous and, in addition, with erect ferruginous hairs down their middle, those of the last visible sternite brownish.

MEASUREMENTS: Length 6.5 mm.; width of thorax 2.25 mm.; length of forewing, including tegula, 8.5 mm.

QUEEN

Unknown.

MALE

Unknown.

TYPE MATERIAL

The holotype was obtained from Baños, Province of Tungurahua, Ecuador, and is in the collection of J. Bequaert.

DISCUSSION

This variety is separated with some hesitation from typical *zonata*, from which it differs mainly in the more completely flavous macu-

lation of its abdomen, the darker banding of which is virtually obsolete. It presents the opposite extreme from a variety of dark abdomen like *caliensis*. In the flavous appearance of the ventral side of its abdomen it resembles variety *brevipilosa*.

DISTRIBUTION

Known from a single specimen collected by William C. MacIntyre at Baños, 1600 to 1900 meters, Province of Tungurahua, Ecuador.

Trigona (Parapartamona) zonata variety
brevipilosa, new variety

WORKER

DIAGNOSTIC CHARACTERS: Structurally and in its sculpturing conforming with the description of the subgenus. The hairs on the scape no longer (many of them shorter) than the scape is wide. Short erect hairs on the clypeus. The eyelash-like hairs fringing the anterior and posterior contours of the hind tibiae ferruginous. The tubercles and tegulae rather bright ferruginous. Merely lateral flavous spots, not a continuous band, on tergites 2 to 5. The under side of the abdomen uniformly flavous.

HEAD (FIG. 71A): Black, including usually the clypeus except for a very narrow brownish stripe along its apical truncation (in one of the paratypes the clypeus has a reddish tinge). Flavous are: the labrum; the mandibles except for their darkened apical edge and black basal prominences; a small trapezium-shaped maculation between the antennal sockets; a clavate maculation along the inner orbit of the eye, rather uniformly wide on its lower half from the level just below the lower extremity of the eye to the level of the antennal sockets, then tapering upward out-slantingly to terminate below the level of the middle ocellus; a stripe on the scape in front, and the second joint of the flagellum below. The genal area mahogany hued. In addition to the silvery gray, appressed, microscopic hairs, there are short, erect, black hairs sparsely present on the clypeus and on the adjacent areas of the sides of the face. The hairs between the antennae, on the front, and on the vertex also black and progressively longer as the vertex is approached.

The hairs on the scape short (not longer, for the most part shorter, than the scape is wide) and largely pale. The erect hairs silvery gray to ferruginous on the lower part of the genal area, on the labrum, and fringing the inferior margin of the mandibles. The genal area silvery gray pruinose as are the clypeus and the sides of face and about of the same density.

THORAX: Black, immaculate except for

as the under side is approached, but even the hairs on the under side no longer than those on the scutellum. The silvery gray tomentum dense on the sides of the propodeum but, in addition, there are numerous erect silvery gray to ferruginous hairs; the appressed silvery gray hairs are a little less dense on the dorsal face of the propodeum.

LEGS: Deep reddish black, with the small tarsal joints of all the legs and the metatarsus

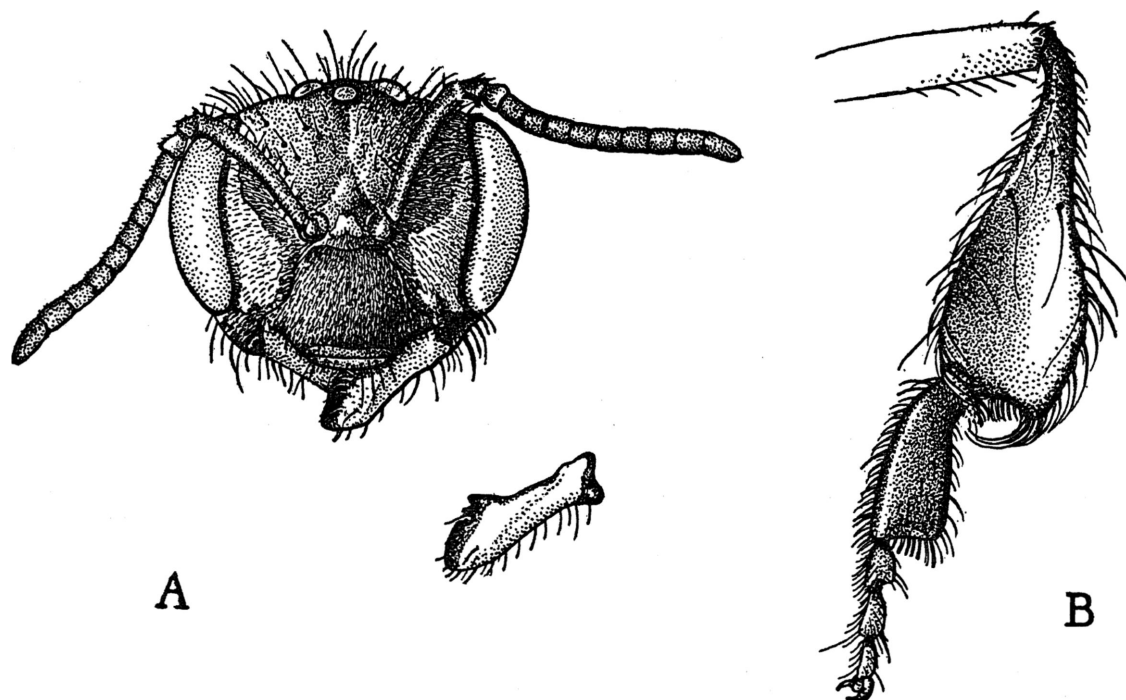


FIG. 71. Worker of *Trigona* (*Parapartamona*) *zonata* variety *brevopilosa*, new variety. A. Head and mandible. B. Tibia and tarsal joints of hind leg. Drawings by Shirley H. Risser.

the ferruginous tubercles. The mesonotum with black bristles along its sides (these bristles tend to be ferruginous basad of the tegulae) and a few sporadic black hairs on the dorsum, but for the most part the mesonotum is covered only with microscopic appressed hairs that give it a dark sericeous sheen. The scutellum, in contrast, with brownish to ferruginous hairs that are nearly as long as the scutellum itself. The mesopleura silvery gray pruinose and, in addition, with erect hairs that grade from ferruginous on the sides of the mesopleura to silvery gray on the under side of the thorax, being progressively longer

of at least the fore legs ferruginous. The hairs of the legs comparable in length and distribution with those noted for the subgenus; the hairs rather uniformly pale, with only the inconspicuous, sparse, short, semi-appressed, black bristles on the outer face of the fore and middle tibiae black. The other hairs for the most part silvery gray, including the short hairs on the upper side of the femora. The eyelash-like hairs fringing the contours of the hind tibiae (fig. 71B) ferruginous as in variety *caliensis*; the brushes on the inner face of the metatarsi pale golden.

WINGS: Lutescent, with the median cell

more strongly yellow. The venation and stigma ferruginous. The tegulae rather bright ferruginous, a little cloudy anteriorly. The number of hamuli per lower wing five in the six wings examined.

ABDOMEN: With the basal depression and most of tergite 1 flavous but a more or less developed dark band, broadest at the middle, along the apex. Tergite 2 not merely with a black apical band but with a longitudinal black stripe running from the middle of the apex to the base, subdividing the basal flavous area into two large spots. Tergites 3 to 5 with not merely a black apical band but also a black basal band, these bands being connected at their middle by a black longitudinal stripe that broadly interrupts a median transverse band of flavous. Tergite 6 flavous. A few pale hairs on each side of the basin-like depression on segment 1. The tergites with an inconspicuous covering of microscopic, appressed, pale hairs, giving these tergites a sericeous sheen in some lights. Semi-erect short black hairs sparsely present on all the tergites, becoming longer and more abundant towards the apex of the abdomen, tergite 6 having the longest hairs. The ventral surface of the abdomen wholly flavous; both the sericeous appressed hairs and the erect hairs silvery gray except those of the last visible sternite, which are ferruginous.

MEASUREMENTS: Length 5 to 6 mm.; width of thorax about 2.25 mm.; length of forewing, including tegula, 8.5 mm.

QUEEN

Unknown.

MALE

Unknown.

TYPE MATERIAL

The holotype and one paratype are at Cornell University; the other paratype is in the American Museum of Natural History. All three were obtained in Colombia.

DISCUSSION

The variety *brevipilosa* differs from *zonata* and the other known varieties of *zonata* in having hairs on the scape that are no longer

(for the most part shorter) than the scape is wide. In agreement with variety *caliensis* but in contrast to typical *zonata* and variety *tungurahuana* the eyelash-like bristles fringing the contours of the hind tibiae of *brevipilosa* are ferruginous, not blackish. The dorsal aspect of the abdomen of *brevipilosa* is similar to that of the typical variety except that the apical black band on tergites 2 to 4 is so expanded upward at its middle that the flavous areas on each side are completely separated from each other. While the tergites of the abdomen in respect to the shrinkage of the flavous areas approach the condition of *caliensis*, in which flavous is dorsally absent, the sternites are unlike those of both *caliensis* and typical *zonata* in being wholly flavous but agree in this respect with the sternites of *tungurahuana*. The presence of short erect black hairs on the clypeus of *brevipilosa* is unusual in members of the *zonata* complex. This variety is distinctive, too, in having the tegulae as well as the tubercles bright ferruginous. Its wings are longer than those of the typical variety and of *caliensis*.

DISTRIBUTION

The three specimens before me are from Colombia, unfortunately without more specific locality data. Two of them were collected on March 11, 1912, and the third on March 15, 1912.

Trigona (Parapatamona) zonata variety
caliensis, new variety

WORKER

DIAGNOSTIC CHARACTERS: Structurally and in its sculpturing conforming with description of the subgenus. The long bristles on the inner side of the scape as well as the eyelash-like hairs fringing the hind tibiae anteriorly and posteriorly are ferruginous. The tergites of the abdomen dark reddish brown with blackish apical rim and devoid of flavous maculation.

HEAD: Like that of typical *zonata*, black, with the clypeus blackish to more or less suffused with reddish and the following parts more or less bright flavous: the labrum; the mandibles except for their darkened apical rim and black basal prominences; a small, trapezium-shaped maculation between the

antennal sockets; sometimes two very narrow short subparallel stripes close together, one on each side of the tapering upper part of the supraclypeus or just beyond; a clavate maculation flanking the inner orbit of the eye to approximately the level of the anterior ocellus, broad below at the level of the clypeus and in-facing, somewhat narrowed at about the level of the base of the antennae and continued thence upward taperingly; a stripe extending part way up the anterior face of the scape. The flagellum blackish above, more or less cloudy ferruginous below. The genal area more or less mahogany hued. No erect bristles on the clypeus or sides of face, only microscopic silvery gray appressed hairs, but erect black hairs (in addition to the microscopic silvery gray appressed hairs) over the front and vertex, where they attain their maximum length, as well as in the supra-clypeal area. The ferruginous bristles towards the base of the inner side of the scape very long and coarse, fully twice as long as the scape is wide. The genal area silvery gray pruinose, its lower part with erect silvery gray hairs. Silvery gray to ferruginous hairs fringe the lower margin of the mandibles and are also on the labrum.

THORAX: Black on the mesonotum and sometimes also on the scutellum, more or less suffused with red on the other thoracic areas and on the propodeum. The mesonotum without erect hairs except for a few short, black, inconspicuous bristles along the sides, but its entire surface with a dark sericeous sheen. In contrast, the scutellum with very long brownish to blackish hairs that are nearly as long as the scutellum itself. The mesopleura silvery gray pruinose and, in addition, with erect ferruginous to silvery gray hairs that increase in length downward and are especially long and dense on the under side of the thorax (but even these hairs are not any longer than those on the scutellum). The silvery gray tomentum dense on the sides of the propodeum, where, in addition, are erect silvery gray hairs; the dorsal face of the propodeum somewhat more lightly covered with silvery gray appressed hairs.

LEGS: Reddish brown, the tarsal joints of all the legs as well as the metatarsus of at least the fore legs ferruginous. The hairs of

the legs comparable in length and distribution with those noted for the subgenus but the hairs rather uniformly pale: the short ones on the upper face of the femora are silvery gray and the eyelash-like hairs fringing the hind tibiae are ferruginous instead of darkish; the brushes on the inner face of the metatarsi pale golden.

WINGS: Lutescent, the median cell somewhat more strongly yellow. The venation and stigma ferruginous. The tegulae sooty reddish with a somewhat lighter reddish pupil. The number of hamuli per lower wing five in the four wings examined.

ABDOMEN: With tergites 1 to 6 deep reddish brown over most of their surface and a somewhat ill-defined darker band along the apex of each. A very few, easily overlooked, short hairs on each side of the more or less ferruginous, basin-like depression on tergite 1. Tergites 1 to 5 with an inconspicuous covering of microscopic, appressed, pale hairs, giving these tergites a sericeous sheen in some lights. Tergite 6 with conspicuous, semi-erect, black hairs, the previous tergites only with an occasional sporadic black stunted hair. The ventral surface of the abdomen in the main reddish brown but with sternite 1 largely flavous and with large flavous spots at the lateral extremities of sternites 2 to 5, supplemented by two more inwardly placed concolorous spots on sternites 2 and 3 of one of the two paratypes; these inner spots obscured in holotype. The ventral surface of the abdomen silvery gray sericeous with, in addition, concolorous erect hairs extending down the middle of the sternites.

MEASUREMENTS: Length about 5.5 mm.; width of thorax about 2.25 mm.; length of forewing, including tegula, 7.75 mm.

QUEEN

Unknown.

MALE

Unknown.

TYPE MATERIAL

Holotype from Cali, Colombia; two paratypes, of which one at least is from San Antonio, Colombia. The type and paratypes are in the American Museum of Natural History.

DISCUSSION

The specimens here given new varietal rank were identified by Friese as his *alfkeni*, described from Venezuela, which in my interpretation is either a synonym or a variety of *zonata* F. Smith. Brief as is Friese's analysis of *alfkeni*, it makes clear that the abdomen of *alfkeni* is flavo-fasciate, a condition out of accord with the present specimens. However, these specimens are far closer to what I conceive as *alfkeni* than are certain other bees on which Friese has likewise placed the label *alfkeni*. He has thus designated certain specimens from Jundiahy in southern Brazil that I interpret as callows of his own *Trigona* (*Partamona*) *testacea* variety *helleri*, and he has furthermore labeled as *alfkeni* a specimen from San Antonio (presumably San Antonio Pass, near Cali), Colombia, that seems to me to be his own *Trigona* (*Partamona*) *testacea* variety *peckolli*.

By its predominantly reddish brown abdomen, which dorsally, at least, is without flavous maculations, the variety *caliensis* differentiates itself not only from typical *zonata* but from the other varieties of *zonata*.

For resemblances and differences between variety *caliensis* and variety *brevipilosa* the reader is referred to the discussion of the latter (p. 435).

DISTRIBUTION

The holotype was collected at Cali, Cauca Valley, Colombia, in 1908 by Fassl. There are two paratypes from Colombia, one labeled San Antonio (presumably San Antonio Pass, near Cali, although the number of places in Colombia that bear the name of San Antonio makes difficult any attempt at localization), the other with a label that cannot be deciphered.

TRIGONA SUBGENUS CEPHALOTRIGONA SCHWARZ

Trigona (*Cephalotrigona*) SCHWARZ, 1940, pp. 10-11, figs. 3-5.

Cephalotrigona, MOURE, 1944a, p. 71.

TYPE SPECIES: *Trigona capitata* F. Smith.

WORKER

DIAGNOSTIC CHARACTERS: Distinguished from the other subgenera of *Trigona* by the following combination of characters: the

unusual sculpturing of the head, which is coarsely punctate and rather shiny on the clypeus, lower part of the supraclypeus, and lower extremity of the sides of the face, but densely granular and dull over the upper part of the head; the peculiar armature of the mandible with its single large tooth at the inner extremity of the apex; the rather unusually large size of the head; the broad hind tibiae.

HEAD (FIG. 72A): Large, emphatically wider than long, although even in length it exceeds the combined length of the mesonotum and scutellum. Eyes somewhat convergent below. The sculpturing very unusual. The prominent clypeus, the likewise prominent supraclypeus to the level of the antennal sockets, and the lower extremity of the sides of the face (the area on each side of the lower half of the clypeus) with large, coarse punctures that are for the most part separated by shiny interspaces. The clypeus of rather uneven surface, often with two more or less distinctly traceable longitudinal furrows on its basal half to two-thirds. The rest of the head in front view dulled by dense granular sculpturing, lusterless compared with clypeus. The upper half of the rather broad genal area finely tessellated, although the tessellation is almost completely concealed by the silvery gray pruinescence. The lower half of the genal area, in contrast, polished, shiny, somewhat streaky, with sparse but rather coarse punctures. The facial quadrangle wide, at its widest towards the upper end about as wide as the distance from the middle ocellus to the apical edge of the clypeus. The clypeus nearly three-fourths as long as it is wide, its sides only slightly divergent apically, with the result that the apico-lateral angles are not very pronounced. The clypeus broadly truncate along its apex. The malar space a little longer than the flagellum is wide. The labrum faintly bigibbous. The mandible (fig. 72A) edentate along the outer two-thirds of its apical edge; the inner one-third with a rather angular emargination, resulting in a single prominent tooth at the inner extremity. The ocelli rather widely spaced, the middle one slightly anterior to the lateral ones, which are somewhat tilted towards their respective compound eyes. The space behind the ocelli broad; the occipital margin emphasized by a

sharp carina, medianly emarginate, that rims that margin for the distance separating the compound eyes. The distance between the lateral ocelli only a little less, in the proportion of about 7 to 8, than that between each lateral ocellus and the nearest compound eye. The flagellum about twice as long as the scape and slightly thicker. The lower half of the face far less hairy than the upper. The hairs on the clypeus few and minute,

roofing the distinctly longer propodeum. The mesonotum, scutellum, and mesopleura, like the upper part of the head, with dense granular sculpturing. The tegulae with dense but distinctly more delicate sculpturing. The propodeum less densely sculptured than the mesonotum, tessellate to punctate laterally and dorsally, but with at least a small, polished, shiny, hairless area posteriorly at the middle. The mesonotum and scutellum

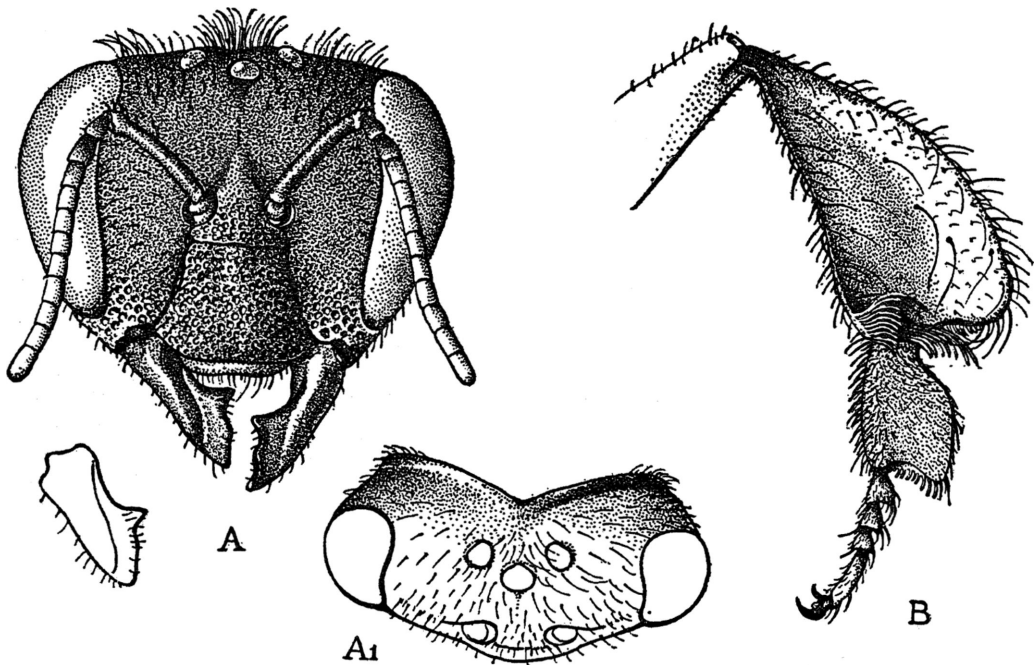


FIG. 72. Worker of *Trigona* (*Cephalotrigona*) *capitata* variety *capitata* F. Smith. A. Head and mandible. A1. Head viewed from above. B. Tibia and tarsal joints of hind leg. Drawings by Shirley H. Risser.

hardly more conspicuous than the inconspicuous microscopic hairs on the scape. The front with hairs of intermediate size; the vertex with hairs that are longer, notably so in the case of the hairs in the triangle formed by the ocelli, and these hairs always black. Hairs fringing the mandibles below likewise long as are those towards the lower shiny part of the genal area.

THORAX: Short, the combined length of the mesonotum and scutellum being somewhat less than the greatest width of the mesonotum near the base. The scutellum very short, rounded posteriorly, not in the least over-

brownish to sometimes grayish sericeous, with, in addition, longish erect hairs anteriorly on the mesonotum and posteriorly on the scutellum, and inconspicuous and usually sparse hairs in the region between. The erect hairs of the mesopleura more abundant and rather long, particularly towards the under side of the thorax. In addition, there are short, appressed, silvery gray hairs on the mesopleura. The entire propodeum dorsally as well as laterally (except for the small, shiny, bare area at the middle posteriorly) covered with silvery gray tomentum and, laterally at least, with erect hairs in addition.

LEGS: Unevenly sculptured, with the tessellation rather uniformly dense, if fine, on the outer face of the fore and middle tibiae and the upper face of the hind femora. The fore and middle femora and the outer face of the hind tibiae (except the rather granular extreme base) tend to be smooth and shiny. The legs progressively longer from front pair to hind pair, the long hind leg being about as extensive as the combined length of the head, thorax, and abdomen. The hind tibia (fig. 72B) emphatically developed, distinctly longer than the combined length of the hind femur and trochanter and almost half as wide towards the apex as it is long, its shape rather clavate with the outer contour strongly convex, the apex rounded on approximately its posterior half. The outer face of the hind tibiae shallowly depressed along its entire length except the extreme base and a slight elevation of the surface at approximately the middle of the joint. The under side of the hind tibia with a slightly raised, plateau-like area along its middle, covered densely with microscopic silvery gray hairs and contrasting with the sharply declivitous shiny area anterior to it and the flat shiny area posterior to it, which are devoid of such microscopic hairs. The hind metatarsi about half as wide as their tibiae, convex posteriorly, approximately straight anteriorly, the outer end of the apex angulate. The hairs rather dense on the coxae, under side of trochanters of front and middle legs (those of hind trochanters scant); longer and denser and covering a larger area on the under side of the fore femora than on the under side of the middle femora; longer on the under side of the middle tibiae than on the under side of the fore tibiae, although the hairs growing posteriorly on the fore tibiae tend to be long; longer on the outer face of the fore metatarsi than on the outer face of the other metatarsal joints. The semi-erect hairs on the outer face of the fore and middle tibiae dwarfed and sparse, these joints seeming at first glance devoid of such hairs although more or less sericeous. Short erect hairs on the upper face of the robust hind femora. The simple hairs fringing the hind tibiae along their anterior and posterior contours short when compared with the width of the joint.

WINGS: With the transverse cubital veins

usually only feebly indicated to absent. The first discoidal cell about nine-tenths as long as the marginal. Number of hamuli per lower wing usually eight, but with a range of from seven to nine.

ABDOMEN: Approximately as wide as the thorax, more or less oval, not trigonate on the ventral side. Tergite 1 polished, with at most an occasional, more or less isolated puncture. Tergites 2 to 6 finely tessellated, densely so on tergites 2 to 5, more sparsely so sometimes on tergite 6, which occasionally has areas devoid of tessellation and shiny. The sternites very finely tessellated. The dorsal side of the abdomen with very few erect hairs. On tergite 1 there are erect hairs at each side of the basal depression and usually also within the depression. Tergites 2 to 5 have microscopic appressed hairs that impart a faintly sericeous sheen, but the few erect hairs that occur on these tergites are usually confined to tergite 5, with a small scattering of undersized hairs more rarely on tergite 4. Tergite 6 with slightly longer hairs, although these, too, are sparse, and in addition usually with more or less silvery gray sericeous hairs. The ventral side of the abdomen with erect hairs sparsely present on the apices of the sternites.

MEASUREMENTS: Length 6.75 to 9 mm. (Ducke recorded specimens even up to 10 mm.); width of thorax 2.75 to 3 mm.; length of forewing, including tegula, 7.25 to 7.75 mm.

QUEEN (VIRGIN)

HEAD (FIG. 73A): Relatively smaller than that of the worker, wider than the mesonotum but not so wide as the distance from the outer rim of one tegula to the outer rim of the other tegula. The sculpturing much less contrasted than in the worker and on the upper half of the head, at least, much less dense, with shiny interspaces among the punctures that make the front only a little less reflective of the light than is the semi-shiny clypeus. The vertex and particularly the genal area (except for the polished and sparsely punctate lower extremity) very finely tessellated. The facial quadrangle wide, approximately as wide as the distance from the middle ocellus to the apex of the clypeus. The clypeus and lower half of supraclypeus prominent;

the clypeus fully two-thirds as long as its greatest width, broadly truncate along its apical middle and briefly receding at each extremity, its sides only slightly divergent apically with the result that the apico-lateral angles are obtuse rather than acute. These angles very remote from the eye, being separated by a space comparable with the width of the mandibles at their base. The malar space much longer than in the worker, the

other lateral ocellus. The occipital margin rather bluntly carinated, not, as in the worker, with a thin, sharply defined, raised edge. The flagellum about twice as long as the scape. The head even less hairy than that of the worker. The clypeus, sides of face, and front devoid or virtually devoid of hair, and even the hairs on the vertex short and inconspicuous (sometimes even absent) as are those along the occipital margin. No erect

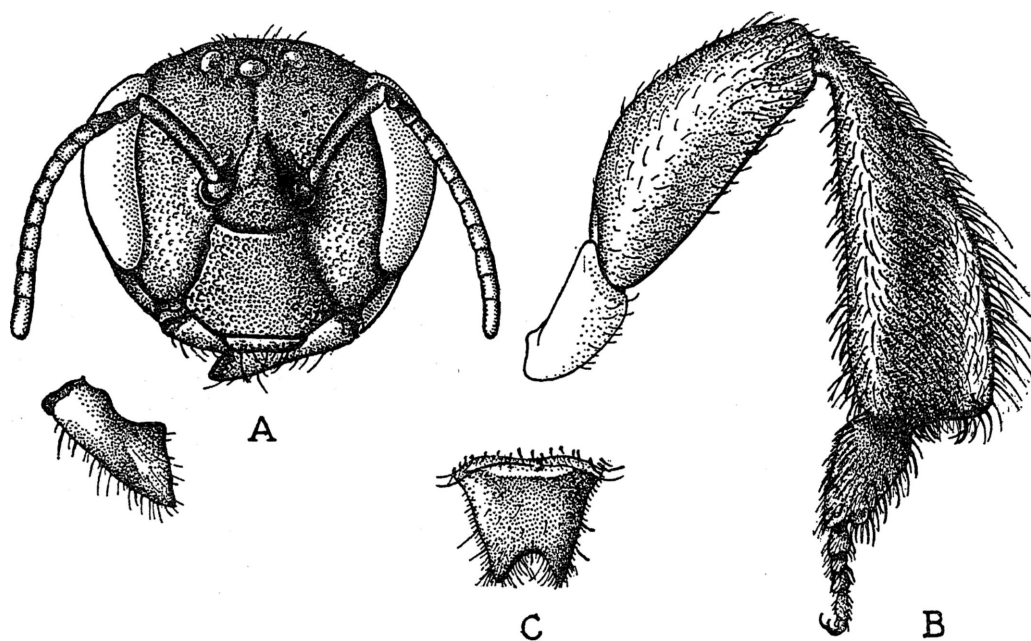


FIG. 73. Queen of *Trigona* (*Cephalotrigona*) *capitata* variety *capitata* F. Smith. A. Head and mandible. B. Trochanter, femur, tibia and tarsal joints of hind leg. C. Sternite 6 of abdomen. Drawings by Shirley H. Risser.

shortest distance between eye and mandible more than twice the width of the flagellum. The eye about four-fifths as long and only about three-fourths as wide as the eye of the worker, being distinctly narrower also than the genal area. The labrum very faintly bigibbous. The mandible (fig. 73A) without the pronounced tooth-like angulation at its inner extremity that characterizes the mandible of the worker. The ocelli rather widely spaced, the middle one slightly anterior to the lateral ones, which are somewhat tilted outward. The distance between each lateral ocellus and the nearest eye greater than that which separates each lateral ocellus from the

hairs on even the lower part of the genal area but the labrum and the inferior margin of the mandible with fairly long hairs.

THORAX: Short, the combined length of the mesonotum and scutellum being less than the greatest width of the mesonotum, which is emphatically wider than is the mesonotum of the worker. The scutellum short, rounded posteriorly, not in the least over-roofing the distinctly longer propodeum. The mesonotum and scutellum not densely granular as in the worker but finely punctate to finely tessellate with some shiny interspaces. The mesopleura with little sculpturing, the upper half with a few punctures, the lower half even

smoother and more shiny. The tegulae with rather dense, delicate tessellation. The propodeum with faint tessellation laterally and dorsally. The mesonotum and scutellum with short appressed hairs over their entire surface and, in addition, with long erect hairs anteriorly on the mesonotum and particularly long hairs, especially posteriorly, over the scutellum (some as long as the scutellum itself). The mesopleura with short appressed hairs as well as with erect hairs, which, short above, tend to become longer towards the under side of the thorax. The entire propodeum dorsally as well as laterally covered with silvery gray appressed hairs, and laterally also with a few erect ones.

LEGS: More robust and hairy than those of the worker. The external face of the fore and middle tibiae more or less finely tessellated; the other joints for the most part without traces of sculpturing. The middle legs intermediate in length between the short fore legs and the long hind legs. The fore tibiae and likewise the middle tibiae notably shorter than their femora, reversing the condition of the hind pair of legs in which the tibiae are emphatically longer than the short but very robust, swollen hind femora, and the combined length of the hind femora and trochanters barely greater than that of tibiae. The hind tibiae (fig. 73B) about five-sixths as wide as those of the worker but somewhat longer. Their shape clavate, the posterior contour somewhat convex but the joint only gradually widened towards the apex, which is rounded posteriorly as well as anteriorly, with a very feeble emargination between. The outer face of the hind tibiae strongly arched anteriorly but flattened towards the posterior margin. The inner face also broadly convex anteriorly but briefly flattened towards the posterior margin. The hind metatarsi about half the width of the hind tibiae, wider at the base than at the apex, their length about that of the small joints of the hind tarsi combined. The hairs on the coxae of moderate length. Those on the under side of the middle trochanters much longer than those on the under side of the fore and hind trochanters, those of the fore trochanters in particular being emphatically shorter than is the case in the fore trochanters of the worker. The largely bare fore and middle femora with

relatively few, inconspicuous hairs compared with the tibiae, but the hind femora with a considerable number of medium to short hairs on their upper and particularly on their outer faces, with fewer hairs on the inner face. All of the tibiae on their external face densely hairy, the hairs being erect or semi-erect and moderately long on the fore and middle tibiae and more pronouncedly long on the hind tibiae (particularly the hairs of the posterior contour) in contrast to the short appressed hairs on the external face of the hind tibiae of the male. The inner face of the hind tibiae with moderately dense, microscopic, appressed, pale hairs over its arched surface. The hairs on the external face of all the metatarsi longer than, and not quite so dense as, the hairs of the metatarsal brushes of the inner face. The small joints of the tarsi also rather hairy.

WINGS: Shorter, or at least no longer, than those of the worker. Transverse cubital veins usually not even feebly indicated, absent (in contrast to the usually at least feeble demarcation in the worker). The first discoidal cell barely shorter than the marginal. Number of hamuli per lower wing seven to eight.

ABDOMEN: Of virgin queen rather bulbous and spherical, with nearly as much depth as width and nearly as much width as length. The abdomen, at its widest on segments 1, 2, and 3 notably wider than the thorax. The three apical tergites sloping downward sharply, with tergite 6 tending to be almost perpendicular. Sternite 6 (fig. 73C) with a bidentate apex jutting out pronouncedly from the end of the abdomen, so much so as to be plainly visible even when the abdomen is viewed from above. Tergite 1 bare and semi-shiny, with shallow but rather large punctures scattered over its surface. Tergite 2 similarly largely bare, semi-shiny, with similar punctation, but its apical edge, at least, fringed with minute hairs. Tergites 3 to 6 densely silvery gray pruinose over their exposed part, which is also densely and very finely tessellated; a very few erect hairs, in addition, at the apex of tergite 6. A few erect hairs along the apex of sternites 1 to 5; sternite 6 more densely and finely hairy.

MEASUREMENTS: Length 8 to 8.5 mm.; width of thorax about 3.5 to 4 mm.; length of forewing, including tegula, about 7 mm.

MALE

HEAD (FIG. 74A): Much wider than long. The eyes, strongly convergent below, larger than in worker. The facial quadrangle much narrower than in the worker, and much narrower below than above, the distance between the eyes near their summits and the distance separating the eyes at their level of closest approximation below being in about

other cases (typical *capitata* and *femorata*) feebly emarginate with a resulting angle on the inner extremity where the worker has a pronounced tooth. Ocelli rather widely spaced, the middle one slightly anterior to the lateral ones, which are somewhat tilted towards their respective compound eyes. The distance between the outer part of the circumference of a lateral ocellus and the far-

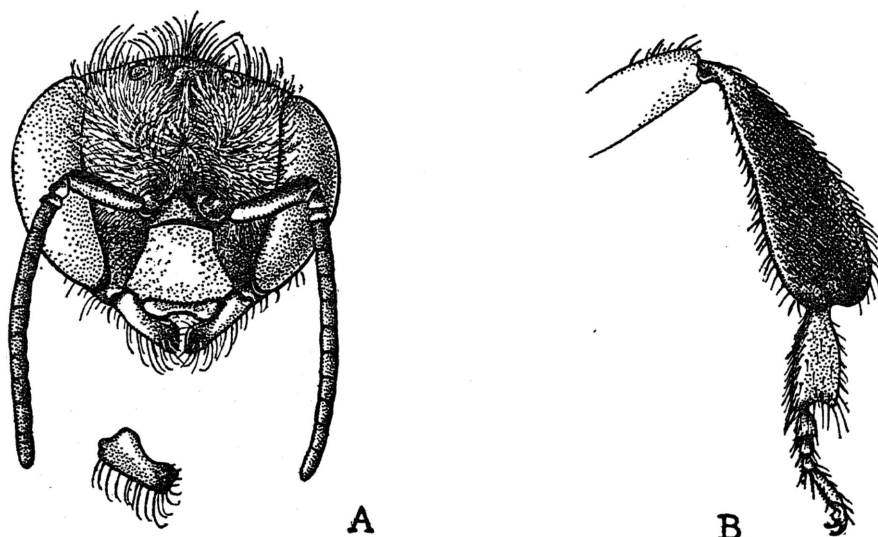


FIG. 74. Male of *Trigona* (*Cephalotrigona*) *capitata* variety *zexmeniae* Cockerell. A. Head and mandible. B. Tibia and tarsal joints of hind leg. Drawings by Shirley H. Risser.

the proportion of 8 to 6. The maculated clypeus and the maculated lower half of the supraclypeus prominent. The clypeus nearly four-fifths as long as its greatest width, its sides obliquely divergent from base to apex, its apex truncate almost from end to end with very little recession at each of its extremities. The malar space at its narrowest only about one-half the width of the flagellum, and the distance between the eye and the antero-lateral angle of the clypeus approximately the width of the flagellum. The maculated labrum somewhat bigibbous, with an emargination along its lower edge at the middle. The mandibles wide at the base and short; when retracted barely more than in contact with each other; their apex only about one-half as wide as their base and in some cases (more especially small specimens of *zexmeniae*) without clear evidence of dentition but in

the point on the circumference of the middle ocellus greater than the distance between the lateral ocellus and the nearest compound eye, the latter distance being approximately double the diameter of an ocellus. The clypeus and the lower maculated part of the supraclypeus punctate to punctate-tessellate, the punctures being rather finer and denser than in the corresponding areas of the worker. The rest of the head viewed from in front dulled with dense granular sculpturing except that sometimes (not always) there is a tiny area of punctation and semi-shininess at the lower extremity of the sides of the face, not so well defined, nevertheless, as in the worker. The genal area with fine but dense tessellation except on its polished lower extremity. The scape, maculated in front, is distinctly thicker than the flagellum but less than one-fourth as long; joint

3 of the flagellum viewed from below indubitably much longer than the combined length of joints 1 and 2 of the flagellum, and, even when viewed from above, at least subequal to them; the apical joint nearly as long as joint 3 of the flagellum. Head distinctly hairy, but the clypeus, at least, has for the most part only minute hairs, much shorter than the not very long hairs of the adjacent parts of the sides of the face and of the supra-clypeus. The hairs on the front and vertex dense and abundant, attaining their maximum length in the region between and behind the ocelli, where they form a rather conspicuous tuft, with the hairs to the right of the center of the middle ocellus curving towards the right and those to the left of the center of the middle ocellus curving towards the left. The hairs towards the lower extremity of the genal area (the polished part) also rather long, longer than the hairs fringing the inferior margin of the mandible, which do not as a rule exceed in length the width of the mandible at the base. The greater part of the genal area (all but the polished part) rather densely silvery gray pruinose. The scape almost devoid of hair, the hair being so sparse and dwarfed that it is easily overlooked.

THORAX: Relatively longer than in the worker. The mesonotum wider than long, but the combined length of the mesonotum and scutellum longer than the width of the mesonotum at its base. The scutellum rounded posteriorly, not extended back over the propodeum, which in dorsal view is a little longer than the scutellum. The mesonotum and mesopleura, like the upper part of the head, with a rather dense granular sculpturing, which is nearly as dense also on the scutellum. The tegulae rather densely but much more delicately tessellated. The propodeum less densely and emphatically sculptured than the mesonotum, tessellate to punctate laterally and dorsally, but with at least a small, polished, shiny, hairless area that is located posteriorly at the middle. Although the thorax tends to be more hairy in the male than in the worker, the hairs are rather apt to be sparse in regions like the mesonotum, where they are sparse and short also in the worker, and are long on the scutellum, again corresponding with the condition in the worker. The entire propodeum dorsally

as well as laterally (except for the shiny bare area previously specified) covered with silvery gray tomentum and, laterally at least, also with some erect hairs.

LEGS: Unevenly sculptured, with the tessellation rather uniformly dense, if fine, on the outer face of all of the tibiae and on the upper face of the hind femora. The fore and middle femora tend to be smooth and shiny above as well as below. The middle pair of legs somewhat intermediate in length between the relatively short fore legs and the longer hind legs. The combined tarsal joints of the middle legs somewhat longer than the combined tarsal joints of the hind legs, the middle metatarsus being nearly as long as the middle tibia. The hind tibiae (fig. 74B) very gradually expanded from base to apex, the apex rounded anteriorly and rounded to subangulate posteriorly. These tibiae not more than one-half the width of those of the worker, slightly arched anteriorly but pinched or flattened towards their posterior rim. The under side of the hind tibiae approximating the structure of that of the worker, with a very slightly raised area along its middle, covered densely with microscopic hairs and contrasting with the sharply declivitous shiny area (with longer and sparser hairs) anterior to it and with the flat shiny area posterior to it. The hind metatarsus a little less than one-half as long as the hind tibia and only about one-half as wide, its sides subparallel. The combined length of the hind metatarsus and the small joints of the tarsi a little less than the length of the hind tibia. The hairs moderately abundant on the coxae and on the under side of the trochanters, sparse and short on the femora, being somewhat longer on the under side of the fore and middle femora than on the upper side, but longer on the upper side of the hind femora than on the under side. The fore and middle tibiae with only microscopic hairs sparsely present on their external face and even these sometimes lacking, but with a posterior fringe of longer hairs and in the case of the middle tibiae with longer hairs also on the under side. The hairs along the anterior and posterior contours of the hind tibiae much shorter than the eyelash-like hairs fringing the hind tibiae of the worker; some minute erect hairs and many microscopic

appressed hairs over the outer face of the hind tibiae. The outer face of the fore metatarsi with distinctly long hairs, much longer than those of the corresponding area of the middle metatarsi; the hind metatarsi with very few erect hairs externally, and these mostly inconspicuous. The brushes on

a more or less distinct fascia along their apex. The dorsal surface of the abdomen with a more or less silvery gray sheen due to the presence of microscopic appressed hairs but the tergites largely devoid of erect hairs, which may occur sporadically but are usually confined to each side of the depression at the

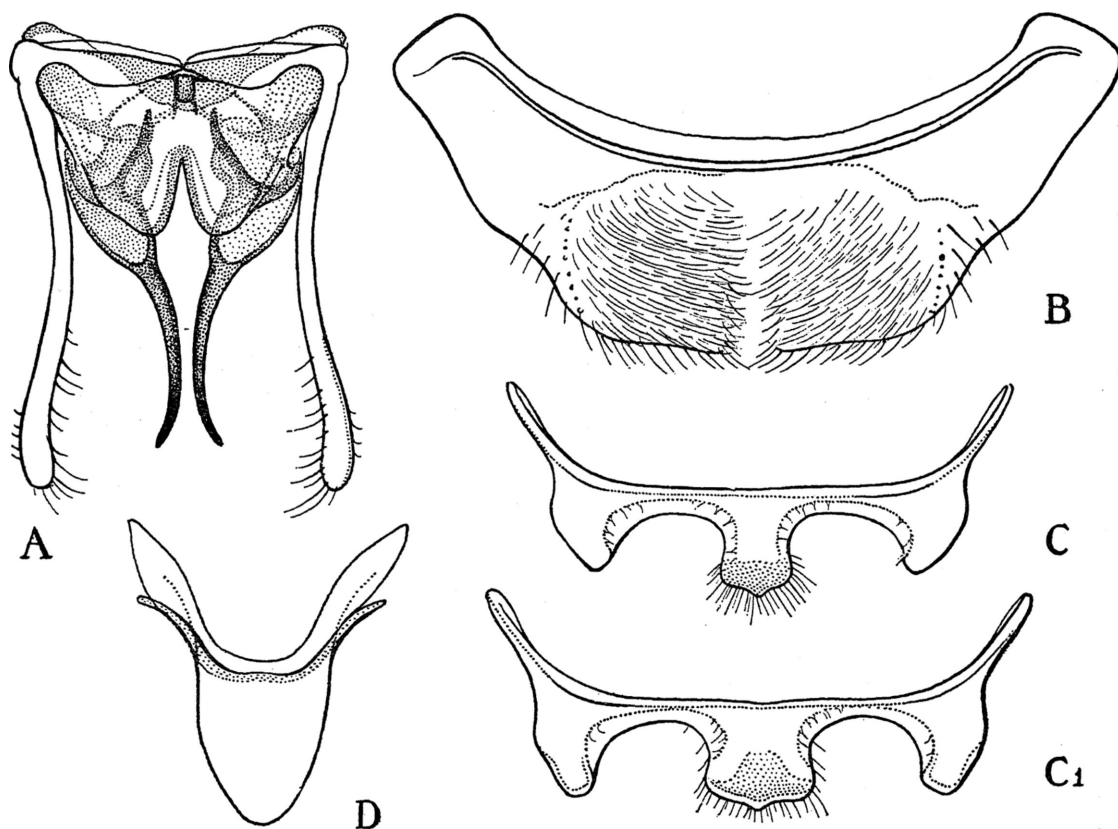


FIG. 75. Abdominal parts of male of *Trigona* subgenus *Cephalotrigona*. A. Genitalia (chitinized parts only), of *capitata* variety *femorata* F. Smith from Pará, Brazil. B. Sternite 5, of *capitata* variety *zexmeniae* Cockerell from Chichen-Itza, Yucatan. C, C1. Sternite 6, respectively, of *capitata* variety *femorata* F. Smith from Pará, Brazil, and *capitata* variety *capitata* F. Smith from São Paulo, Brazil. D. Sternite 7, based on specimen of *capitata* variety *femorata* from Pará, Brazil. Drawings by Shirley H. Risser.

the under side of the metatarsi dense but short.

WINGS: Similar to those of the worker, with the number of hamuli ranging from seven to 10.

ABDOMEN: Nearly as wide as the thorax and rather oval. Tergite 1 polished, without or sometimes with evidences of punctation on the posterior half. The subsequent tergites finely and densely tessellated, with usually

base of tergite 1, and to tergites 6 and 7, fringing the latter. The ventral side without erect hairs but sericeous, densely so on sternites 3 to 5, the exposed parts of which form a continuous silky surface. The usually wholly or largely concealed sternite 6 (fig. 75C, C1) tridentate, with the median tooth exceptionally wide and bluntly tipped [somewhat resembling the corresponding tooth of sternite 6 of the male of *Trigona* (*Tetragona*)

dorsalis Smith] and the lateral teeth also well developed and in-pointing. Sternite 7 (fig. 75D) of rather elongate, somewhat sugarloaf shape, deeply emarginate at its base. The genitalia (fig. 75A) with the median plate large and deeply and abruptly emarginate at the apical middle.

MEASUREMENTS: Length 5.75 to 9 mm.; width of thorax 2.5 to 2.75 mm.; length of forewing, including tegula, 6.75 to 7.25 mm.

DISCUSSION

The subgenus *Cephalotrigona*, which Moure recently (1944a, p. 71) raised from subgeneric to generic rank, is especially differentiated from the other subgenera of *Trigona* by the characters of the worker as summarized at the beginning of the description of that caste. Not only is the kind of contrasted sculpturing of the head in this caste unique, but the unidentate condition of the mandible is very unusual. The Old World subgenera *Dactylurina* and *Heterotrigona*, which also have only one tooth on the mandible of the worker, are in other respects so utterly different from *Cephalotrigona* as to preclude the thought of close relationship.

The male of *Cephalotrigona* is also differentiated from the other subgenera by the somewhat contrasted character of the sculpturing of its head.

The queen has the last visible sternite of the abdomen strongly bidentate at the apex, although this condition, more feebly developed, is present also in certain other *Trigona*, for example, *Trigona* (*Scaura*) *latitarsis* Friese and *Trigona* (*Oxytrigona*) *tataira* Smith.

Ducke (1925, p. 351) placed *capitata* F. Smith, here considered the type species of *Cephalotrigona*, in one of the two main subdivisions of his Division III. In the other subdivision of Division III he included insects that are here assigned to the subgenera *Trigona*, *Tetragona*, *Oxytrigona*, and *Scaura*. My own feeling is that *Cephalotrigona* is far removed from such advanced subgenera as *Trigona* and *Tetragona*, and that it is more nearly affiliated with some of the forms of rough as opposed to smooth chitin. As in the subgenera *Schwarziana*, *Parapartamona*, and *Partamona*, the present subgenus has more or less hair not only on the sides of the pro-

podeum, where it is usual in stingless bees, but also on the dorsal region of the propodeum, where in so many subgenera there is a large bare area. The presence of hair in the dorsal region of the propodeum is particularly marked in *Melipona*. In contrast, the subgenera *Trigona*, *Tetragona*, *Oxytrigona*, *Scaura*, *Plebeia*, *Hypotrigona*, *Paratrigona*, *Scaptotrigona*, and *Nannotrigona*, as well as the genus *Lestrimelitta*, all have the hairless dorsal region sharply demarked from the more or less densely hairy sides of the propodeum.

Hermann von Ihering (1903, p. 207) noted briefly a nest of *Cephalotrigona capitata* that was located in a tree trunk and had a simple flight hole of inconsiderable size. Subsequently, however, he gave a more detailed account (1912, pp. 1, 44-45) based on a second nest of *capitata*, likewise obtained from the trunk of a tree. Von Ihering was particularly impressed by the great size of the honey and pollen containers, some of which measured 52 by 40 mm., and by the fact that, although there were numerous virgin queens in the nest, there was no evidence of royal cells. From these and other observations on the same nest he drew the following conclusion: "The species in question (*capitata*) forms in regard to its biology a transition stage to *Melipona*. Morphologically connected with *Trigona*, it nevertheless constructs the gigantic provision containers of the larger species of *Melipona*, is docile like these, builds its batumen plates of clay and has a wide portal, which, however, is not, as in the case of *Melipona*, made of clay but of resin and wax. The most interesting thing by all odds is, nevertheless, the rearing of young queens in ordinary worker cells."

Marianno (1911, p. 86) spoke of *capitata* as a subterranean species, which is somewhat puzzling, but did not give details regarding the internal structure of its nest and made no note of the cells in which the queens are reared.

Von Ihering's impression that the queens do not develop in royal cells was based on the fact that, although in excess of 20 young queens were present in the nest he examined, there were no traces of specialized cells from which they might have emerged. But this is merely negative evidence. In refutation may

be cited the careful observations of Salt (1929, pp. 441-442) based on a nest of *capitata* variety *sexmeniae* Cockerell in a hollow limb: "The one tier counted consisted of 375 cells, and the entire nest (there were eighteen tiers of cells) contained about 5000. Individual cells measured 7 mm. long and 4.2 mm. in diameter, and were about two-thirds filled with the larval food. Those containing male bees were indistinguishable from those occupied by workers, and were scattered indiscriminately in the comb in the ratio of about one male to twelve worker cells (September 27). Only two queen cells were found, one containing a pupa, the other a larva. These were situated with the male and worker cells in the tiers but were readily distinguishable by their larger size and rounded instead of flat ends."

KEY TO THE VARIETIES OF *Trigona*
(*Cephalotrigona*)

WORKERS

1. The thorax wholly black, entirely devoid of maculations on the mesonotum, axillae, and scutellum. Tergites 1 to 5 completely or almost completely black, but tergite 6 and most or all of the under side of the abdomen a sharply contrasting ivory color or cream color. The hairs on the ventral side of the abdomen usually pale. The two longitudinal furrows on the clypeus rather deep. The mandibles and labrum rather bright reddish . . . *capitata* variety *eburneiventris*, new variety. Not having the above combination of characters; almost invariably with at least a short stripe on each side of the mesonotum . . . 2
2. The mesopleura more or less invaded by red, sometimes largely or wholly red. The yellow stripe along each side of the mesonotum wide and strong, confluent or virtually confluent with a strong and concolorous triangular maculation occupying virtually the entire surface of the axillae; usually a more or less strongly developed stripe of similar coloration on the scutellum posteriorly. The tegulae ferruginous to sometimes yellowish. The femora bright pale rufotestaceous, usually briefly touched at the apex (especially in the case of the hind femora) with sharply contrasted black *capitata* variety *femorata* F. Smith. The mesopleura without red 3
3. The abdomen dull reddish fulvous, the tergites more or less darkened narrowly along the apex . . . *capitata* variety *sexmeniae* Cockerell

The abdomen predominantly black
. *capitata* variety *capitata* F. Smith

QUEENS

(Because of the far from complete representation of queens of *Cephalotrigona*, it has seemed preferable to omit a key to the royal caste.)

MALES

(Too much uncertainty beclouds the identification of the males to warrant a key for this caste.)

Trigona (*Cephalotrigona*) *capitata* variety
capitata F. Smith

- ? "Mumbúca," COELHO DE SCABRA, 1799, pp. 100, 102.
? "Mumbucú," PERTY, [1833], p. 28.
? "Mumbúco," GARDNER, 1846, p. 328.
? "Mumbúco," GARDNER, 1849, p. 249.
Trigona capitata F. SMITH, 1854, p. 409.
? *Melipona bilineata* and "Mumbuca," DRORY, 1874, pp. 281, 282.
? "Mumbuca," ANONYMOUS, 1878a, p. 73.
? "Mumbuco," GRONEN, 1881a, p. 54.
Melipona mombuca, PECKOLT, 1893, p. 580 (not *Trigona mombuca* F. Smith).
Melipona mombuca, PECKOLT, 1894, p. 90 (not *Trigona mombuca* F. Smith).
Melipona capitata, DALLA TORRE, 1896, p. 576.
Trigona capitata variety *virgilii* FRIESE, 1901, p. 268.
Trigona capitata variety *virgilii*, H. VON IHERING, 1903, p. 207.
Trigona capitata variety *virgilii*, H. VON IHERING, 1904b, p. 386.
Trigona capitata, COCKERELL, 1905, p. 323.
Trigona capitata, DUCKE, 1908b, p. 80 (specimens from Brazilian States of São Paulo and Santa Catharina).
Trigona capitata, DUCKE, 1910b, p. 367.
Trigona capitata, MARIANNO, 1910d, p. 8.
Trigona capitata, STRAND, 1910, p. 558.
Trigona capitata, MARIANNO, 1911, pp. 8, 85-86 (in part).
Trigona capitata variety *virgilii*, MARIANNO, 1911, pp. 8, 87.
Trigona capitata, BERTONI, 1911, p. 143 (identified by H. Friese).
Trigona capitata, H. VON IHERING, 1912, pp. 44-45.
Melipona virgili, DUCKE, 1916, pp. 80, 82.
Trigona capitata, STRAND, 1916, p. 139.
Trigona capitata variety *virgilii*, FRIESE, 1917, pp. 288, 299.
Trigona capitata variety *virgilii*, LUTZ AND COCKERELL, 1920, p. 496.
Trigona capitata, COCKERELL, 1923a, p. 451.

Trigona capitata, LUTZ, 1924a, pp. 205, 207, 209, 216, 220, 221, 222.

Melipona capitata variety *virgili*, DUCKE, 1925, pp. 389, 391, text fig. S, pl. 4, fig. 15.

Melipona capitata, BISCHOFF, 1927, p. 290.

Trigona capitata, SCHWARZ, 1932a, pp. 244, 247, 253, 258, 260.

Trigona capitata, MAIDL, 1934, p. 578.

Melipona capitata, MAIDL, 1934, p. 663.

"Mombuca" or "Mumbuca," R. VON IHERING, 1940, pp. 520, 880.

Trigona (Cephalotrigona) capitata variety *capitata*, SCHWARZ, 1940, pp. 10-11, figs. 3-5.

Cephalotrigona capitata, MOURE, 1944a, p. 71.

WORKER

DIAGNOSTIC CHARACTERS: Dark form, with not only the head and thorax but also the abdomen predominantly blackish. The thorax more or less maculated with yellowish on at least the mesonotum. The erect hairs on the ventral side of the abdomen usually black.

HEAD (FIG. 72A): Predominantly black, to the inclusion usually of the clypeus, which is, however, sometimes suffused more or less with reddish and in some instances (callows) has a pale, inverted, T-shaped maculation (see discussion). The labrum and mandibles either reddish or (particularly the mandibles) partly reddish and partly blackish; in extreme cases both labrum and mandibles wholly black (a specimen from Uberaba). Base and sometimes apex of scape, antennal sockets reddish; flagellum beneath usually deep reddish to ferruginous. The erect hairs black on clypeus, sides of face, front, and vertex, ochraceous to sometimes brownish on the lower margin of the mandibles and silvery gray or predominantly silvery gray on the lower part of the genal area; the pruinescence dense and silvery gray on the upper part of the genal area, and there are also less conspicuous, microscopic, silvery gray, appressed hairs usually traceable on the sides of the face and front.

THORAX: Predominantly black, with a variable amount of yellowish maculation. In the type specimen the faint stripe along each side of the mesonotum extends from a point opposite the middle of the tegula to the axillae, which are devoid of maculation as is the scutellum. From this condition of limited maculation there are gradations to the other extreme (characteristic especially of the

Peruvian, Bolivian, Venezuelan, British Guianan, and Surinam specimens before me) in which a broader stripe runs from a point opposite the base of the tegulae to the axillae, which have a strong triangular maculation, and in addition there is frequently a stripe posteriorly on the scutellum; sometimes even the tubercles are somewhat maculated. The erect hairs black on the mesonotum, scutellum, and usually on at least the upper part of the mesopleura, and there are likewise dark erect hairs among the silvery gray tomentum of the sides of the propodeum.

LEGS: Dark rufo-testaceous to blackish, with the tarsal joints more or less ferruginous. The hairs of the coxae silvery gray, those of the under side of the trochanters also tend to be gray but often they include at least some hairs that are sooty, particularly in the case of the middle pair, and the hairs on the under side of the fore and middle femora vary from gray to blackish and are sometimes of mixed character. More invariably black are the hairs on the fore and middle tibiae, those fringing the hind tibiae (fig. 72B) and those on the metatarsal joints externally. Within, the fore metatarsal joints tend to have golden brushes; the middle and hind pair have brushes that are copper colored to black.

WINGS: Fairly transparent, tinged with yellowish; stigma and venation ferruginous to light brownish. Tegulae usually fuscous. Number of hamuli per lower wing ranges from seven to nine. Of a total of 150 wings counted, 127 had eight hamuli, 15 had seven hamuli, eight had nine hamuli, an average of 7.96.

ABDOMEN: Black or brownish black over the first five tergites (tergite 1 sometimes slightly reddish) and usually black also on tergite 6, which, however, sometimes has the apical half yellowish. Sometimes there is traceable a faint, narrow, indistinct vestige of banding also on the other tergites. The erect hairs on tergites 5 and 6 black; in addition, tergite 6 frequently is rather densely covered with silvery gray, appressed, microscopic hairs. The venter likewise blackish or dark brownish with the erect hairs prevailing black except on tergite 1, where they tend to be silvery gray.

MEASUREMENTS: Length 6.75 to 8 mm. (10 mm., according to Ducke); width of

thorax about 3 mm.; length of forewing, including tegula, about 7.75 mm.

QUEEN (VIRGIN)

DIAGNOSTIC CHARACTERS: Mainly rust colored to cloudy ferruginous in contrast to the almost wholly black worker and predominantly black male; the mesonotum black, but even it is rather widely banded laterally with yellow.

HEAD (FIG. 73A): More or less dark rust colored on sides of face, vertex, genal area, and upper half of supraclypeus, with the clypeus, lower half of supraclypeus, labrum, and malar space more or less ferruginous. The hairs on the labrum, those near the apex of the mandibles and those fringing the mandibles beneath, as well as the inconspicuous stunted hairs on the vertex and occipital edge pale, those on the vertex sometimes lacking.

THORAX: With the mesonotum black except for a rather wide, full length stripe of pale yellow along each of its sides and sometimes two concolorous hair-fine parallel lines running from the base of the mesonotum for a brief distance apicad. The mesopleura rust colored above, reddish black below; the axillae and scutellum rust colored, more or less clouded with black. The propodeum paler, ferruginous to faded yellow. The hairs of the thorax silvery gray.

LEGS: Rust colored to mainly ferruginous, with the fore and middle tibiae and to some extent the fore femora reddish black. The hairs of the legs mainly or wholly pale. (Fig. 73B.)

WINGS: Fairly transparent, with the stigma and venation ferruginous. The tegulae ferruginous to rust colored. Number of hamuli per lower wing ranges from seven to eight.

ABDOMEN: Mainly rust colored to fulvous over its tergites, with a paler ferruginous area on each side of tergite 1. The ventral side of the abdomen mainly ferruginous. The short hairs fringing tergites 2 to 5 and the erect hairs at apex of tergite 6 pale; tergites 3 to 6 silvery gray pruinose. The hairs at the apex of sternites 1 to 5 pale; sternite 6 silvery gray pruinose (fig. 73C).

MEASUREMENTS: Length about 8.5 mm.; width of thorax about 4 mm.; length of forewing, including tegula, about 7 mm.

MALE

DIAGNOSTIC CHARACTERS: The mesonotum (except for a yellowish stripe bordering each of its sides) and the mesopleura black. The axillae maculated but a yellowish stripe rimming the scutellum posteriorly sometimes absent. The legs usually more or less darkened not only on their tibiae but also on their femora, but the character is not constant.

HEAD: Black, with the clypeus, a trapezium-shaped to triangular figure on the lower half of the supraclypeus, a stripe on the scape anteriorly, the labrum, and the mandibles (except for their usually darkened or reddened apical edge) pale yellow to cream colored. The flagellum dark above, and more or less ferruginous below. The hairs (both erect and appressed) silvery gray except those of the vertex, which, in rare instances also silvery gray, tend usually to be yellowish to brownish.

THORAX: Mainly black, the mesopleura wholly so. A yellowish stripe (wider and longer than is usual in the workers from corresponding localities) along the side of the mesonotum, extending from a level somewhat basad of the tegulae to the apex of the mesonotum, there to unite with the triangular maculations of the axillae. In some cases the stripe is continued thence along the posterior rim of the otherwise black scutellum, but in other instances (most of the specimens from São Paulo) the black scutellum is without maculation. The tubercles more or less yellow to ferruginous, sometimes black. The propodeum black. The hairs of the mesopleura silvery gray and sometimes also those of the mesonotum (specimen from Tarata, Bolivia), but usually the erect hairs of the mesonotum are brownish to fuscous and this applies also to the hairs on the scutellum. The propodeum with silvery gray to whitish tomentum as well as concolorous erect hairs.

LEGS: Variable in coloration. In some cases at least the fore pair are a rather light brown, more or less in contrast with the darker middle and hind legs, but in other cases the legs are rather uniformly dark brown from pair to pair. The femora in some specimens not so dark as their tibiae and metatarsi but in others with little or no dif-

ferentiation between the color of these joints. On the whole, however, the legs tend to be cloudy brownish to blackish. The hind tibiae dark, with usually a pale maculation at the base; a small pale maculation also frequently present at the base of the fore and middle tibiae. The small joints of the tarsi and sometimes also the metatarsal joint (more especially in the case of the front legs) ferruginous. The hairs of the first pair of legs silvery gray except for the more or less golden metatarsal brushes and sometimes a few dark hairs on tibiae posteriorly. The hairs of the second pair of legs, with the exception of the golden metatarsal brushes, rarely all silvery gray (specimen from Tarata, Bolivia), more often with the tiny hairs on the external face of the middle tibiae, the longer hairs posteriorly on that joint, and the hairs externally on the middle metatarsi in part or wholly dark. The hairs of the third pair of legs rarely all silvery gray (specimen from Tarata) with the exception of the golden metatarsal brushes, more often with black or blackish hairs on some of the following parts: upper face of hind femora, the posterior contour of hind tibiae but rarely the anterior contour, and sparsely on the outer face of the hind metatarsi.

WINGS: Fairly transparent, tinged with yellowish, with ferruginous to light brownish stigma and venation. Tegulae usually ferruginous to brownish, frequently with a pupil; sometimes fuscous. In the small series available the hamuli ranged from seven to 10 per lower wing. Of the 19 wings examined, there were 13 that had eight hamuli, five that had seven hamuli, and one that had 10 hamuli, an average of 7.84.

ABDOMEN: Viewed dorsally, black (tergite 1 sometimes a little less dark than the succeeding ones). The apex of tergites 2 to 6 narrowly and sometimes feebly banded with a cream-colored stripe which on tergites 2 to 5 tends to have a knob-like thickening at each of its lateral extremities. The abdomen, viewed ventrally, brownish to sometimes paler. The few hairs on each side of the basal concavity of tergite 1 pale, the sparse short hairs on tergite 6 and the hairs fringing tergite 7 usually black but silvery gray in the specimen from Tarata. Sternites 1 and 2 sparsely, and sternites 3, 4, and 5 densely,

silvery gray sericeous. Sternite 6 is depicted in figure 75C1.

MEASUREMENTS: Length 7.5 to 9 mm.; width of thorax about 2.75 mm.; length of forewing, including tegula, 6.75 to 7 mm.

TYPE MATERIAL

Trigona capitata was described from Brazil, without more specific locality reference. F. Smith's type is in the British Museum (Natural History). What Friese regarded as a distinct variety, *virgilii*, but which is here interpreted as a synonym of typical *capitata*, was obtained from Blumenau in the Brazilian State of Santa Catharina.

DISCUSSION

Throughout *capitata* there is considerable variability, and the lines of demarcation are not easy to establish with finality because of borderland specimens. Even in what is here grouped under typical *capitata* there is considerable range of variability. Ordinarily the stripe along each side of the thorax is in the worker narrow and short, extending from the axillae to the level of the middle of the tegulae, and the axillae and scutellum are immaculate. This is the condition in the type specimen of *capitata* (a worker) in the British Museum. Friese (1901, p. 268) erected the variety *virgilii* on the basis of its more feeble thoracic maculation, but numerous specimens identified by Friese as *virgilii*, including some from the type locality, Blumenau, seem to me to be fully as maculated, in some instances more extensively maculated, than is F. Smith's type specimen. It is true that Friese in his description of *virgilii* indicated that sometimes the thoracic maculations are wholly lacking. But this condition I have been able to note in none of the South American specimens before me, and it would seem to be a very unusual extreme. On the other hand, it is one of the characters that, taken in conjunction with other characters, seems to me to make distinctive the Mexican bee that is named in this paper *capitata* variety *eburneiventris*.

In contrast to the workers of limited maculation on the thorax are others that not only have a full-length stripe along the sides of the mesonotum but that, in addition, have the axillae more or less completely maculated

(a condition shared by all of the males I have examined) and a stripe posteriorly on the scutellum. This condition is particularly prevalent in the Peruvian, Bolivian, and British Guianan workers here reported upon and is shared also by the few specimens from Surinam.

The workers of fuller thoracic maculation are apt to approach the condition that is the usual one for the male in this part of the body.

In erecting the variety *virgilii* Friese sets down as one of the characters the "dark black-brown" body color. This fact and the even more convincing evidence offered by the fact that in subsequent identifications he assigns the name *virgilii* to specimens of dark abdomen somewhat irrespective of the extent of the thoracic maculation make me think that Friese perhaps interpreted *capitata* as the variety with reddish abdomen. Certain it is that Ducke so interpreted F. Smith's *capitata*, for Ducke alludes to the "bicolored typical form" (1925, p. 390).

Undoubtedly to be interpreted as callows are certain specimens from Turrucare, Costa Rica, which have a clearly defined, pale yellowish maculation of inverted T-shape on the clypeus. This maculation stands in sharp contrast to the dark areas of the clypeus that flank the stem of the T and to the dark mandibles. In several of these specimens, however, there are few other traces of the callow state. A single specimen from São Paulo, Brazil, and a specimen from Kamakusa, British Guiana, share the coloration noted in these specimens from Turrucare. That the specimens with the pale inverted T on the clypeus are callows receives substantiation from the fact that several of them are exuding wax, an indication that they are young individuals.

In certain respects the specimens from Surinam are distinct from typical *capitata*. While sharing the more fully maculated thorax of many of the specimens from Bolivia and Peru, they have exclusively or predominantly silvery gray erect hairs instead of blackish on the mesopleura, and the erect hairs on the under side of the abdomen are also silvery gray. Reversing the condition noted in the putative callows discussed in the last paragraph, these Surinam specimens

have a black inverted T on the clypeus with a dull reddish brown area on each side of the stem of the T, but such a condition of the clypeus is shared also by many specimens from Kamakusa, British Guiana, that include also an individual with pale inverted T, indicating that the pale T and the dark T are probably merely two stages of development.

The description of the queen is based on specimens from Cabeceira do Uruçú, State of Matto Grosso, Brazil, that Ducke identified as *capitata* variety *virgilii*, here considered a synonym of typical *capitata*. The queens are unaccompanied by workers, but I assume that Ducke's identification must have been influenced by the presence of workers from the same nest. As a matter of fact, the queens in question more nearly approximate the worker of *capitata* variety *femorata* in their coloration than they do the worker of the typical form. Such a distinctive character as the division of the mesopleura into an upper reddish region and a lower, more blackish region is shared by these queens and the workers of *femorata*. It is easy, however, to be misled by such resemblances in the coloration, and particularly in *Cephalotrigona* (although the tendency is more or less prevalent also in the royal caste of other stingless bees) there is a disposition of the queen to be lighter colored and more callow-like in appearance than is the mature worker.

Nests of *capitata* located in tree trunks have been reported by Ambrosetti (1895, p. 699) under the popular name of "mombuca," by H. von Ihering (1903, p. 207), and by Bertoni (1911, p. 143), who stated that the bees prefer large trunks. A second nest described by H. von Ihering (1912, pp. 44-45) was in the spacious interior of a trunk that was 47 cm. in thickness. On the other hand, Marianno (1911, p. 86) spoke of the nests as being subterranean, although he had made no observations on the bees in a natural state and had only limited opportunity to observe them when domesticated.

The flight hole H. von Ihering (1903, p. 207) referred to as "of inconsiderable size"; Marianno (1911, p. 86) pronounced it "little noticeable," Bertoni (1911, p. 143) described it as "a small rounded hole." In a report regarding his second nest H. von Ihering (1912,

pp. 44-45) spoke of "the simple flight-hole," 10 by 12 mm. in diameter, which consisted of a hard resin.

The nest last mentioned measured 60 to 70 cm. in height by 20 to 28 cm. in diameter. The lower part was shut off by a batumen plate 6 cm. in thickness consisting of earth. Above and laterally from the batumen there followed the involucrum, or brood envelope, consisting of numerous fine wax membranes; the involucrum enveloped the entire mass of combs and separated from the combs the provision pots that were located above the brood chamber. Worthy of comment was the irregular arrangement of the brood combs, only two of these being entire, all the others being divided and separated by the involucrum mass.

Allusion has been made previously to H. von Ihering's failure to discover royal cells of *capitata*. As his statement has received emphasis in the literature, with the implication that this bee, like true *Melipona*, does not construct a differentiated queen cell, it is in order to emphasize again that von Ihering's observations are quite at variance with those of Salt for *capitata* variety *zexmeniae* Cockerell (Salt, 1929, pp. 441-442). Young queens were present to a number in excess of 20 in von Ihering's nest, and he argued from this that there should have been evidence of abandoned royal cells if royal cells are used. However, it is a fact, to which von Ihering himself bore testimony (1903, p. 184), that "cells that have been once used are in the case of the Meliponids never used a second time, but are at once carried off" and, while this citation is applied to the cell of the worker, it seems not unlikely that the same practice is pursued also in the case of the royal cells and may well account for the absence of queen cells in this nest.

The pollen pots and honey pots in the nest noted by H. von Ihering (1912, p. 45) were enormous. Some were actually 52 mm. by 40 mm., rather thin walled and frequently isolated, being connected only by strands with the neighboring pots.

According to Bertoni, nests of *capitata* have in their lower part a disk of earthen matter (1911, p. 143). One wonders whether this is comparable to the so-called scutellum

found in nests of *Trigona* (*Trigona*) *ruficrus* (Latreille).

Various writers have noted the pacific behavior of *capitata*. According to H. von Ihering (1903, p. 207), it was not unduly disturbed even when its nest was opened. Marianno (1911, p. 86) pronounced it "timid and docile."

Possibly in part because of its unaggressive behavior, it is a species that has on several occasions, at least, been domesticated. The only colonies (two) known to Marianno were domesticated colonies, and Bertoni (1911, p. 143) spoke of having succeeded in domesticating *capitata* "with good results."

If, however, *capitata* does not usually react belligerently towards man, it apparently is not devoid on occasions, at least, of a martial spirit where other stingless bees are concerned, for Bertoni indicated that a colony of *capitata* would decimate itself in continual warfare if placed near other bellicose species. On the other hand, other observers have recorded *Cephalotrigona* as living apparently in amity with its neighbors, or at least not decimating itself. Salt (1929, p. 435) told of a colony of *capitata* variety *zexmeniae* Cockerell, that shared a tree hollow with two other species of stingless bees, *Melipona interrupta* variety *salti* Schwarz, and *Trigona* (*Trigona*) *amalthaea* (Olivier), and Vincent Baker wrote me regarding a colony of typical *capitata* that similarly had as neighbors in a hollow tree a colony of *Melipona favosa* variety *favosa* (Fabricius) and one of a species of *Scaptotrigona*.

Reports regarding the honey of *capitata* are somewhat contradictory. Marianno (1911, p. 86) reported it "of good quality," and that, according to Ducke (1925, p. 390), was the verdict also of Miranda-Ribeiro. On the other hand, H. von Ihering (1912, p. 45) found its taste not pleasant, somewhat sour. Bertoni (1911, p. 143) commented to the effect that *capitata* is one of the largest producers of honey, and he obtained from one nest alone no less than 16 liters. Among the plants visited by *capitata* are *Waltheria viscosissima* and *Stylosanthes angustifolia* (Marianno, 1911, p. 86).

A popular name for this bee is "mombuca" or "mumbuca" (R. von Ihering, 1940, pp.

520, 535, 880). Dücke (1916, p. 80; 1925, p. 343; 1945, p. 62) listed as other native names for *capitata* the following: "mombucão" (in the Brazilian State of Matto Grosso, on the authority of Miranda-Ribeiro), and "papa-terra" (in southern Brazil, on the authority of J. Marianno). Ambrosetti (1895, p. 699) gave "eiruzú" as another name for "mombuca" in the Alto Paraná of Misiones. Bertoni (1911, p. 143) indicated a slightly variant spelling in citing "eiruzú" as the designation used in Paraguay for *capitata* and noted that the word is of Guaraní derivation. "Mombuca," which H. von Ihering (1904b, pp. 382, 386) indicated as a name of Tupi (or, more strictly speaking, Guaraní) origin, is, according to von Ihering, indicative of one who digs and hence is an appropriate name for an insect that establishes its nest, according to Marianno at least, in the ground. But another bee that persistently builds in the earth is the stingless bee to which F. Smith gave the name *Trigona mombuca*. It is an insect very different from *capitata*, belonging to a different subgenus (*Tetragona*), and it is a pity that two *Trigona* should thus be competing for the same designation, the one having it as a matter of scientific standing, the other largely because of popular use.

Mr. Vincent A. Baker informed me by letter that the natives applied the term "negrito" to the specimens of *capitata* that he took near San Felix on the Orinoco River, Venezuela.

DISTRIBUTION

Typical *capitata*, broadly interpreted, is a form of very extensive distribution, occurring from Mexico to southern Brazil and the contiguous region of Misiones in northern Argentina. The earlier records are from southern Brazil and it would seem likely that F. Smith's type also was derived from this region. Strand (1910, p. 558) reported it from Trinidad. Bertoni (1911, p. 143) recorded it from Guaraní, and Dücke (1916, p. 82; 1925, p. 391; 1945, p. 64) under the designation variety *virgilio* from Puerto Bertoni, all localities in Paraguay. A record from Bolivia is contributed by Strand (1916, p. 139). Cockerell (1923a, p. 451) in reporting *capitata* that was collected along the Berbice River in British Guiana, noted also its occurrence in

localities in Panama and Costa Rica, from which Friese had reported it as well (1917, p. 288). Dücke (1916, p. 82; 1925, p. 391; 1945, p. 64) reported from Tacubaya, Mexico, the "in part reddened form" that he misinterpreted as true *capitata*, but I have seen also a specimen of the typical form from Mexico although most of the Mexican specimens that have come to my attention are assignable to the new form *eburneiventris*. Dücke (1916, p. 82; 1925, p. 391; 1945, p. 64) also cited specimens from Peru, of which there are many instances before me. Other countries represented among the material here reported upon are Argentina, Bolivia, Venezuela, Surinam, and Honduras. The Brazilian states here included are Matto Grosso, Minas Gerais, São Paulo, and Santa Catharina, from all of which I have seen specimens. Dücke (1916, p. 82; 1925, p. 391; 1945, p. 64) reported specimens of *virgilio* (here considered a synonym of typical *capitata*) also from the Brazilian areas of Acre Territorium, Goyaz, and Paraná. Dücke does not include the State of Pará in the list of states where *virgilio* occurs and I have failed to find among the limited number of workers of *capitata* before me from that state any that I would assign to the typical variety. The Pará specimens I interpret as variety *femorata*.

The localities represented among the material before me are:

MEXICO: No. 2387 (C. F. Baker).

COSTA RICA: San Carlos, 1902; Esparta, Sept. 18, 1905 (F. Knab); Colombiana, 400 feet, Aug. 23, 1923 (J. A. G. Rehn); Siguires en Guácima, No. 172 (A. Alfaro); Turrucare, June 29, 1937 (A. Alfaro).

HONDURAS: Monte Cristo (W. M. Mann); Puerto Castilla, March 27, 1924; Prieta, April 7, 1924.

VENEZUELA: State of Bolívar: Near San Felix, July 1, 1946 (V. A. Baker).

SURINAM: Sint Barbara Plan, Surinam River, April 15, 1927; Ongelijk, Para River, May 1, 1927; Moengo, Boven Cottica River, May 16, 1927 (Cornell Univ. Exped.).

BRITISH GUIANA: Kaieteur, Feb. 18, 1921; Kamakusa, Sept., 1922, including males, and Jan., 1923 (H. Lang); Kartabo, July 29, 1924 (J. F. W. Pearson).

PERU: Hda. San Juan, Colony of the Perené, June 23, 1920; El Encanto, Putumayo District, Aug. 25, 1920.

BOLIVIA: Tarata, 1900, including male (Priewasse); Tumupasa, Dec. (W. M. Mann); Cavinass, Feb., 1922 (W. M. Mann); Ivon, Río Beni, Feb., 1922 (W. M. Mann).

BRAZIL: State of Matto Grosso: Cabeceira do Uruçú (Ribeiro), queens; Chapada (probably Sant' Anna do Chapada, near Cuyabá); Cicade Branco, Pôrto Velho, Aug. 20, 1943 (Mark Taylor). State of Minas Gerais: Uberaba, 1900 (Draenert). State of São Paulo: São Paulo, 1897, including males (von Ihering); Jundiahy, 1899, including queen. State of Santa Catharina: Blumenau, Oct., 1898 (Virgil); Nova Teutonia, Nov. 11, 1939 (F. Plaumann).

ARGENTINA: Iguazú Falls, Jan. 20-22, 1920 (Cornell Univ. Exped.).

Trigona (Cephalotrigona) capitata variety
eburneiventer, new variety

WORKER

DIAGNOSTIC CHARACTERS: Wholly black thorax; dorsal side of abdomen deep brownish black to black except for ivory to cream-colored tergite 6 and the concolorous venter. The hairs on the venter pale.

HEAD: Predominantly black, but the labrum and the mandibles, except for their black basal prominences and narrow apical edge, bright red. Base of scape, antennal sockets, and flagellum beneath (the apical joint also usually above) more or less ferruginous. The microscopic erect hairs on clypeus black, the much longer erect hairs on front and vertex likewise black, those on the lower margin of mandibles ferruginous, those on lower part of genal area silvery gray; the pruinescence on upper part of genal area silvery gray, as are the less dense, appressed, microscopic hairs on the sides of the face and front.

THORAX: Wholly black, without any maculation on the mesonotum. The erect hairs black on the mesonotum, scutellum, and upper part of mesopleura, grading into silvery gray below and on the under part. A semicircle of fluffy white tomentum about the tubercles supplemented by a contiguous patch posteriorly. The silvery gray tomentum on the propodeum far more conspicuous than the appressed silvery gray hairs on the mesopleura; the erect hairs interspersed among the tomentum on the sides of the propodeum silvery gray to slightly yellowish.

LEGS: Very dark reddish black to in places

wholly black but with the small joints of the tarsi and the posterior angle of the apex of the hind metatarsi rather bright ferruginous. The hairs silvery gray on the coxae, trochanters beneath (except sometimes the middle pair, which may have more golden hairs), and the under side of the fore and middle femora. The hairs black on the upper face of the hind femora, external face of fore and middle tibiae, fore tibiae posteriorly, middle tibiae beneath, fringing the hind tibiae, and all the metatarsi externally. The metatarsal brushes range from golden (fore pair) to copper colored or blackish (hind pair).

WINGS: Fairly transparent, tinged with yellowish, with bright ferruginous stigma and venation. The tegulae deep reddish black. Number of hamuli per lower wing ranges from seven to eight. Of the 16 wings available for examination, 13 had eight hamuli and three had seven hamuli, an average of 7.81.

ABDOMEN: With tergites 1 to 5 deep brownish black to black, but the exposed part of tergite 6, in contrast, an ivory to cream color. The under side of the abdomen entirely (or for the most part) concolorous with tergite 6. The erect hairs on tergites 5 and 6 black. The microscopic, appressed, silvery gray hairs on tergite 6 denser and more conspicuous than those which impart a faint sheen to the first five tergites. The erect hairs of the under side of the abdomen usually silvery gray (darker in two specimens collected between Temascaltepec and Tejuipilco).

MEASUREMENTS: Length 6.75 to 8 mm.; width of thorax about 3 mm.; length of forewing, including tegula, 7.75 mm.

QUEEN

Unknown.

MALE

See discussion.

TYPE MATERIAL

Holotype (from Cuernavaca, State of Morelos, Mexico) in the American Museum of Natural History. Paratypes in the American Museum of Natural History, the British Museum (Natural History), the United States National Museum, Cornell University, and the California Academy of Sciences.

DISCUSSION

This variety, which seems to be confined to localities in southern Mexico, appears to me to have a combination of characters that entitle it to recognition. It is true that some of the Brazilian specimens of typical *capitata* have a partly pale tergite 6. Even F. Smith's type of *capitata* is of this character. In typical *capitata*, however, the ventral side of the abdomen of the worker inclines to brown or black and is not, as in *eburneiventer*, completely or all but completely cream colored. The total absence of thoracic maculations is highly unusual in *capitata* but is the rule in *eburneiventer*. Finally there are the pale erect hairs on the under side of the abdomen of *eburneiventer*, which occur only very exceptionally (some specimens from Surinam) in typical *capitata*. The mainly blackish dorsal aspect of the abdomen and the completely black and unmaculated mesonotum readily separate this variety from all the other varieties except the typical form.

There is before me a single male collected August 3, 1938, by L. J. Lipovsky at Cuernavaca, State of Morelos, Mexico. As workers of *eburneiventer* are known from this locality (although no workers were obtained with the lone male), it would seem probable at first thought that the male is assignable to this variety. If so, then the male of *eburneiventer* is hardly to be separated from the male of typical *capitata*, for, unlike the worker, the specimen in question has a stripe along each side of the mesonotum, the axillae maculated, and even a maculation on the posterior half of the scutellum.

DISTRIBUTION

Several of the specimens of variety *eburneiventer* before me are from Cuernavaca, in the Mexican State of Morelos, although they were collected at different times and by different individuals. However, the form is not confined to Cuernavaca or even to the State of Morelos, as the following records of distribution indicate. All the known records are, however, from southern Mexico.

MEXICO: State of Morelos: Cuernavaca, June (H. H. Smith), without date (Crawford). State of Guerrero: Tepetlapa, 3000 feet, June (H. H. Smith); Venta de Zopilote, 2800 feet, Oct. (H. H.

Smith). "Mexico," without more specific locality (C. F. Baker). Tejupilco-Temascaltepec, June 29, 1933 (H. E. Hinton and R. L. Usinger).

Trigona (Cephalotrigona) capitata variety *zexmeniae* Cockerell

Trigona zexmeniae COCKERELL, 1912c, pp. 313-314.

? *Trigona capitata*, FRIESE, 1917, pp. 289, 299.

? *Trigona capitata*, LUTZ AND COCKERELL, 1920, p. 496 (Costa Rican specimen).

Trigona zexmeniae, LUTZ AND COCKERELL, 1920, p. 501.

Trigona capitata variety *zexmeniae*, SALT, 1929, pp. 441-442 (identified by H. F. Schwarz).

Trigona capitata variety *zexmeniae*, BEQUAERT, 1932, p. 17 (identified by H. F. Schwarz).

Trigona capitata subspecies *zexmeniae*, SCHWARZ, 1932a, p. 244.

Trigona capitata, MAIDL, 1934, p. 664.

Trigona capitata zexmeniae, MICHENER, 1946, p. 185.

Trigona zexmeniae, COCKERELL, 1946, p. 204.

WORKER

DIAGNOSTIC CHARACTERS: Thorax black except for narrow stripe along sides of mesonotum to, rarely, the inclusion of the axillae. Abdomen deep reddish fulvous with usually tergites 3, 4, and 5, and sometimes also 2 and 6, banded at the apex with black. Erect hairs on under side of abdomen black.

HEAD: Predominantly black. The labrum sometimes ferruginous and sometimes black. The mandibles rufo-piceous with at least their basal prominences and apical rim black, sometimes extensively black. The clypeus usually black but sometimes more or less red (holotype) or deep red with an inverted black T (specimens from Motzorongo, Vera Cruz, Mexico). The antennal sockets ferruginous, as is the scape at the base and sometimes at the extreme apex, more rarely with a dull reddish stripe in front running from base to apex; the flagellum black above and usually dark reddish to sometimes ferruginous on the under surface with the apical joint often tipped with ferruginous. The erect hairs black on clypeus, front, sides of face, and vertex; those on the lower part of the genal area and fringing the mandibles below more variable, sometimes largely silvery gray to ochraceous, but often reddish or brownish. The pruinescence dense and silvery gray over the upper part of the genal area, and less

conspicuous, microscopic, silvery gray, appressed hairs usually on the sides of the face.

THORAX: Black, with a thin yellowish stripe along each side of the mesonotum; the axillae often entirely black but sometimes with a trace of maculation, very rarely fully maculated (specimens from La Chorrera, Panama). The erect hairs black on the mesonotum, scutellum, and at least the upper part of the mesopleura; in rare cases the erect hairs are black over the entire mesopleura but more often the black hairs are replaced by silvery gray hairs towards the under side of the thorax. Also there are dark erect hairs among the silvery gray tomentum on the sides of the propodeum.

LEGS: Rather variable in coloration. In some specimens dark rufous to blackish (including type material), but even in these cases there is a tendency for the basal joints to the inclusion of the femora to incline somewhat more to rufous, the tibiae and metatarsi, on the other hand, more to blackish. In other specimens the contrast between the lighter basal joints and the darker tibiae and metatarsi is more emphatic, particularly in the case of the hind legs, the rufo-testaceous femora of which are in such specimens only a little less bright than the corresponding femora in variety *femorata*. The small joints of the tarsi, or at least the apical tarsal joint, more or less ferruginous. The hairs silvery gray to blackish on the coxae and on the under side of the trochanters (except the middle trochanters the hairs of which are tawny), sometimes silvery gray but in other cases dark on the under side of the fore and middle femora. The erect hairs on upper side of hind femora black. The short hairs externally on the fore and middle tibiae, the longer hairs on the fore tibiae laterally, and the still longer hairs on the under side of the middle tibiae black as are the hairs fringing the hind tibiae anteriorly and posteriorly and the hairs on the outer face of the metatarsal joints. The brushes on the inner face of the metatarsi sometimes golden but as a rule, and particularly in the case of the hind pair, copper colored to black.

WINGS: Fairly transparent, tinged with yellowish, with bright ferruginous to light brownish stigma and venation. The tegulae deep reddish brown to fuscous. The number

of hamuli per lower wing ranges from seven to nine. Of the 36 wings examined, 32 had eight hamuli, three had nine hamuli, and one had seven hamuli, an average of 8.06.

ABDOMEN: Dull reddish fulvous dorsally as well as ventrally, with tergites 3, 4, 5 almost invariably, tergite 2 frequently, and tergite 6 more rarely banded narrowly at the apex with fuscous (see discussion). The erect hairs on tergites 5 and 6 black, as are also the erect hairs on the sternites.

MEASUREMENTS: Length 7 to 9 mm.; width of thorax 3 mm.; length of forewing, including tegula, 7.75 mm. (See discussion for measurements of certain workers of smaller size from Río Frio, Colombia.)

QUEEN (GRAVID)¹

DIAGNOSTIC CHARACTERS: Mainly fulvous to here and there cloudy reddish or blackish. Differs from the queen of typical *capitata* especially in the coloration of the mesonotum, which is fulvous to reddish traversed longitudinally by two posteriorly diverging black stripes that at their anterior end bend outward towards the tegulae and then backward along the inner margin of the pale yellow stripe that borders the sides of the mesonotum, outlining an almost completed oval.

HEAD: With the clypeus, lower half of supraclypeus, labrum, lower extremities of sides of face, malar space, and lower part of genal area, scape in front, flagellum beneath, fulvous to reddish with here and there vestiges of yellow and also of black (basal prominences and apical edge of mandibles, lower boundary of malar space, etc.). The upper part of the head deep blood red to blackish, with the vertex and genal area largely black. The hairs on the labrum, those near the apex and along the inferior margin of the mandibles, and the short hairs on the vertex, ferruginous to pale brownish.

THORAX: With the mesonotum colored as indicated in the condensed prefatory description. The axillae and scutellum blackish. The mesopleura cloudy red. The propodeum of a more faded and less vivid color than the fulvous to bright reddish mesonotum (probably a variable condition, for it is not shared

¹ It is possible that this queen, from Río Frio, Colombia, is not the queen of *sexmeniae* but constitutes yet another variety of *capitata* (see discussion).

by a virgin queen from the same nest). The hairs of the thorax ochraceous to silvery gray.

LEGS: Rather unevenly dark reddish and brownish, but the inner face, at least, of the hind femora, of the tibiae and of the metatarsi a rather unclouded red, and the base of all the tibiae externally also pale red. A darkish area towards the apex beneath of all of the femora, but more especially in the case of the hind pair. The hairs in the main pale, but darker from some angles than from others and undoubtedly including some blackish hairs, especially in the dark areas above of the hind femora and on the hind tibiae.

WINGS: Fairly transparent, tinged with yellowish, with bright ferruginous stigma and venation. Tegulae bright fulvous. Number of hamuli in the unmutated wing of the physogastric queen eight (in the virgin queen from the same nest, the wings have, respectively, seven and eight hamuli), an average of 7.67.

ABDOMEN: Pale fulvous both dorsally and ventrally, but a little cloudy basally on tergite 1. The short hairs fringing apically tergites 2 to 5, the longer erect hairs at the apex of tergite 6, and the erect hairs at the apex of sternites 1 to 5 all pale; tergites 3 to 6 and sternite 6 silvery gray pruinose.

MEASUREMENTS: Length of physogastric queen about 11 mm. (of which the abdomen accounts for about 6 mm.); width of thorax about 3.5 mm.; length of forewing, including tegula, about 7 mm.

The length of a virgin queen from the same nest about 8 mm.

MALE

See discussion.

TYPE MATERIAL

Described from Quiriguá and Gualan, Guatemala. Holotype in the American Museum of Natural History, paratypes in the British Museum (Natural History) and the United States National Museum.

DISCUSSION

The worker of this variety can be readily differentiated from the worker of the typical variety and from variety *eburneiventer* by the color of the abdomen, which is dull reddish fulvous in contrast to the black or brownish

black appearance of at least tergites 2 to 5 of typical *capitata* and of *eburneiventer*. In respect of the coloration of its abdomen it is somewhat comparable to variety *femorata*, but the presence usually of black bands on the abdominal tergites, the absence of red on the pleura, and the more feeble yellow thoracic bands bordering the mesonotum will assist in separating at least the worker of *zexmeniae* that is thus characterized from the other form.

A series of workers from northern Yucatan collected by Gaumer is doubtfully placed in *zexmeniae*. One of the individuals in this series has dark legs and dark bands apically on the abdominal tergites and readily qualifies as *zexmeniae*. Several others have the abdomen reddish fulvous but lack the darker bands or have merely fragments of these bands, but these specimens, too, seem closer to *zexmeniae* than to the other forms.

Evidence of dark banding on the abdominal tergites is also lacking in specimens from La Chorrera, Panama, which likewise depart from what is usual in workers of *zexmeniae* in having fully maculated axillae. Indeed in these Panamanian workers not only is the darker banding lacking but it is replaced by a very narrow band of yellow, somewhat as in typical *capitata*. The specimens are so close to *zexmeniae*, however, that I should hesitate giving them an independent status. Somewhat the same comment applies to specimens from Cienaga, Colombia, which likewise are somewhat aberrant.

Specimens assignable to *zexmeniae* may occur even in the same nest with typical *capitata*. Thus a series from Sigiuares en Guácima, Costa Rica, collected by A. Alfaro, includes with a predominant number of typical *capitata* certain specimens that must be referred to variety *zexmeniae*. The specimens so designated have in most cases the hind femora red on the upper side, but they are too mature in appearance, I think, to encourage the interpretation that they are callows of typical *capitata* or that, given time, they would acquire the dark abdomen of that form.

The furrows on the clypeus of the worker of *capitata* differ somewhat in profundity from specimen to specimen. In the type material of *zexmeniae* these furrows are superficial,

not so deep as in the type of *capitata* and distinctly shallower, for instance, than in the specimens of variety *femorata* from Río Negro, Bolivia.

The difficulty of making sharp separations within *Cephalotrigona* will be obvious from the comments of this discussion but for long I hesitated whether or not to give an independent status to the bees of this subgenus that Salt collected at Río Frio, Colombia, and that I determined as *zexmeniae* (Salt, 1929, pp. 441-442). These bees are, in the first place, of smaller size. The workers have a length of 6.75 to 8 mm.; width of thorax 2.75 to 3 mm.; length of forewing, including tegula, 7.25 to 7.75. Their hamuli, too, average fewer than in the Central American specimens assigned to *zexmeniae*. Of 44 wings of the Río Frio workers examined, 38 had eight hamuli, and six had seven hamuli, an average of 7.86 compared with the average of 8.06 for *zexmeniae* in other regions, but too much weight should not be accorded to this disparity in equipment as the number of specimens counted is too small to permit a decisive conclusion.

What makes interpretation of these Río Frio workers difficult is that most of them are obviously callows, with the pale inverted T on the clypeus that characterizes the callow also in typical *capitata*. These callows compare in coloration with other callows of *zexmeniae* from Central America, but the remarkable thing is that they also are deceptively close in their coloration and in the character of their markings to the adult physogastric queen from the same nest, even to the inclusion of the exceptionally maculated mesonotum as described for that queen, a character shared also by the virgin queen before me.

I should have been distinctly hesitant to designate the physogastric queen from Río Frio as *zexmeniae* had she been taken independently of the colony, so different is her general coloration from that of the mature worker of *zexmeniae* collected elsewhere. The same statement applies with equal force to the virgin queen. While the peculiar maculation of the mesonotum of this individual would tempt one to think of it as a callow, the fact that the virgin queen shares this peculiarity with the mature physogastric queen

rather supports the belief that this is the standard coloration of the royal caste.

In addition to the workers from Río Frio that are obviously callows there are a few workers from that nest that are of more mature appearance. These workers have only the median one-third of the mesonotum reddish, the rest black, somewhat paralleling the condition in *Trigona* (*Oxytrigona*) *talaira* variety *mediorufa* Cockerell. It is possible that they represent the culmination of coloration of their kind, but I think it more likely that they, too, are callows although of an advanced stage, approaching the complete coloration represented by the mature *zexmeniae*. If, on the other hand, the tripartite coloration of the mesonotum that I have indicated (namely, medianly red flanked on each side by a comparable area of black) is the final coloration, then these Río Frio specimens would have to rank as another variety and the queen that is here described as the royal member of *zexmeniae* would have to be transferred to that new variety.

The males from Río Frio are also smaller than a series of males from Chichen-Itza, Yucatan. Again I am giving independently the measurements of these Río Frio males, so as to keep them distinct from the Chichen-Itza males assigned to *zexmeniae*: length 5.75 to 7 mm.; width of thorax about 2.5 mm.; length of forewing, including tegula, about 6.75 mm.

In the Río Frio series of males, of a total of 28 wings examined, only seven had as many as eight hamuli; the remaining 21 had seven hamuli. The average was 7.25.

The measurements for the Chichen-Itza males are: length 7 to 9 mm.; width of thorax 2.75 mm.; length of forewing, including tegula, about 7.25 mm.

The number of hamuli in the 36 wings of specimens from Chichen-Itza that I examined was as follows: only three specimens had as few as seven hamuli, 31 had eight hamuli, one had nine hamuli, and one had the unusual total of 10 hamuli, an average of eight. The average for the males from Río Frio and Chichen-Itza combined is 7.7 as against 7.84 for the males of typical *capitata*.

In all the males from Río Frio and in nearly all of the males from Chichen-Itza the pattern on the mesonotum is identically that

described for the physogastric queen (and also for the virgin queen) from Río Frio. The preponderance of male specimens that bear this stamp of identity in pattern with the thoracic pattern of the mature queen tends to encourage the belief that this pattern may be the usual condition also in the male. However, the fact that there are one or two males from Chichen-Itza that have lateral obscuration of the mesonotum and only the median one-third definitely red gives strong support to the belief that the individuals of predominantly reddish thorax (laterally as well as medianly) are callows even though in all other respects they seem to have attained their full coloration. In *Trigona* (*Cephalotrigona*) *capitata* variety *zexmeniae* Cockerell, it is apparently the mesonotum that is most tenacious in its retention of the coloration of the callow, still bearing the earmarks of that state after all the other parts of the body have attained the color of maturity.

It is also in order to emphasize that while in callows of many species the scutellum is one of the last areas to acquire the coloration of the mature adult, in these males of *zexmeniae*, as in the callows of the worker of that variety, the scutellum is black even though the mesonotum is predominantly red. This combination of red or largely red mesonotum with black or at least dark scutellum occurs also in a bee of the subgenus *Scaptotrigona* that Friese designated *hellwegeri* (1900a, p. 389). The thoracic pattern of *hellwegeri* is an almost exact duplication, so far as the mesonotum is concerned, of that of the callow of *zexmeniae*, except that in *hellwegeri* the lateral yellow stripes are absent.

A further circumstance to cause perplexity in variety *zexmeniae* is that the male, if one excepts coloration of the mesonotum (here interpreted as that of the callow rather than of the mature adult), is not to be separated from the male of typical *capitata*. Thus in *zexmeniae* there would seem to be a sexual dichromatism, with the worker characterized by a reddish fulvous abdomen, the male by a mainly black abdomen with apical bands. Thus one is again forced to weigh the possibility that the worker of *zexmeniae* is itself merely a callow stage of typical *capitata*. The instance already referred to, where specimens of both typical *capitata* and *zex-*

meniae occur in the same nest, certainly gives ground for hesitation in making final interpretations. Nevertheless, it seems on the whole wiser in the present state of our knowledge to retain *zexmeniae* as well as *femorata* as varietal names within *capitata*.

Even if for the moment it be assumed that *zexmeniae* is merely a different developmental stage of *capitata* and that given time to complete its coloration it would ultimately be indistinguishable from *capitata*, we are still faced with a puzzling situation. In some nests the callows would then apparently all have arrived at maturity except for the coloration of the abdomen; in other nests, by way of complete contrariness, the abdomen of the several members of the population would have taken on the deep tone of the adult while the mesonotum still flaunted the coloration of the callow. Such a difference in the sequence of development seems unlikely and, even if the end result were the same, would still prompt doubts whether the respective nest populations could be considered in all respects as one.

The variety *zexmeniae* has been observed visiting the following flowers: *Zexmenia virgulta* Klatt, *Vernonia aschenborniana* Schauer (Cockerell, 1912c, pp. 313-314) and *Tribulus cistoides* Linnaeus (Salt, 1929, p. 442).

Salt (1929, pp. 441-442) gave a detailed and illuminating account of a nest from Río Frio, Colombia, part of which I have already quoted in the discussion of the subgenus *Cephalotrigona*. The nest occupied a space between 8 meters and 8.6 meters from the ground in a hollow limb. Above it in the same hollow limb was a nest of *Trigona* (*Trigona*) *amalthaea* (Olivier) and below it a nest of *Melipona interrupta* variety *salti* Schwarz. The nest of *capitata* variety *zexmeniae* had a length of 58 cm. and a width varying from 12 cm. to 15 cm.; the flight hole measured 12 mm. by 7 mm. There were 18 tiers of cells, horizontally arranged and supported one above the other by cerumen pillars. The honey pots, though large, did not attain the dimensions of those measured by H. von Ihering (1912, p. 45) in a nest of typical *capitata*, being 3.5 or 4 cm. long and 2.5 cm. in diameter, with their walls of thin cerumen "often adjacent so that it was impossible to take out one pot without opening others," a

condition again at variance with at least many of the provision containers noted by von Ihering, which, instead of being contiguous, were separated by pillars. The honey pots vastly outnumbered the pollen pots, only four of the latter, externally indistinguishable from the honey pots, being observed in the nest examined by Salt. "Honey-pots filled the basal 15 cm. of the cavity and extended up two sides of the comb to a height of 29 cm. One or two pots flanked the cell tiers at the top, and the remaining 18 cm. of length, minus that taken up by [an] intruding piece of wood, was packed with others." The batumen plates, which H. von Ihering in his account of typical *capitata* referred to as being entirely of earthen material without admixture of wax even though easily molded between the fingers, were in the case of variety *zexmeniae* made of "hard and brittle cerumen containing much earth." Salt referred to the involucrum as "well-developed."

The honey from this nest was, according to Salt, "clear, rather thin, and somewhat tart." The disposition of the bees was pacific, for they "did not attack in any way when the nest was broken open." Similarly typical *capitata* is said to be unaggressive, at least towards man.

In addition to the nest observed by Salt mention should be made also of one observed by Bequaert (1932, p. 17). As were all the nests of the subgenus *Cephalotrigona* except those recorded by Marianno (1911, p. 86), the nest noted by Bequaert in Chichen-Itza, Yucatan, was in a tree hollow, but, instead of being rather high in the tree, it was only about 2 feet above the ground. "On June 4, many males were observed sitting on the leaves of bushes near the entrance or hovering in the vicinity." These males are undoubtedly the very ones discussed earlier. All of the specimens collected seem to be callows, and their gathering in numbers outside the nest recalls the aggregates of immature individuals observed in the case of certain other species (see Introduction, pp. 56-59).

DISTRIBUTION

The variety *zexmeniae* occurs for the most part in Mexico and Central America. Described from Quiriguá, Guatemala, it is known also from the localities below specified:

MEXICO: Jacubaya, 1900 (Barrett). State of Vera Cruz: Atoyac, April (H. H. Smith); Motzongro, Feb. 7 and 13, 1892 (H. Osborn); Córdoba, Jan. 4 and 20, 1908 (F. Knab) and (Crawford). State of Yucatan: Valladolid (Gauger); Chichen-Itza, including males, June, 1929 (J. Bequaert); Mérida, 1936.

BRITISH HONDURAS: Belize (Baker).

HONDURAS: Prieta, April 5-7, 1924.

GUATEMALA: Chiquimulilla, 300 meters (René Lichy).

COSTA RICA: Pozo Azul, June 15, 1902 (M. A. Carriker, Jr.); San José, May 25 (H. Schmidt); Siguíares en Guácima, No. 172 (A. Alfaro).

NICARAGUA: Chontales (Janson).

PANAMA: La Chorrera.

CANAL ZONE: Balboa, March 20, 1915 (T. Hallinan); Barro Colorado, Feb. 18, 1929 (C. H. Curran), and March 4, 1933 (F. E. Lutz); Corozal, Jan. 19, 1929 (C. H. Curran).

COLOMBIA: Department of Magdalena: Ciénaga, Aug. 20, 1927, at *Tribulus cistoides* Linnaeus (G. Salt); Río Frio, Sept. 24, 1927, queens, males, workers (G. Salt).

Trigona (Cephalotrigona) capitata variety *femorata* F. Smith

Trigona femorata F. SMITH, 1854, pp. 410-411.

Melipona femorata, DALLA TORRE, 1896, p. 578.

Melipona capitata, DUCKE, 1901, pp. 49, 64.

Melipona capitata, DUCKE, 1902a, pp. 325, 419.

Melipona (Trigona) capitata, DUCKE, 1902b, pp. 289, 299-300.

? *Trigona capitata* variety *rufa*, SCHULZ, 1904b, p. 820.

? *Trigona capitata*, DUCKE, 1908b, p. 80 (Amazonian specimens).

Melipona capitata, DUCKE, 1916, pp. 26, 80-83, pl. 6, fig. 17 (in part).

? *Trigona capitata*, COCKERELL, 1923a, p. 451 (Pará specimens).

Melipona capitata, DUCKE, 1925, pp. 341, 389-391, pl. 4, fig. 15 (in part).

Melipona capitata, DUCKE, 1945, pp. 23, 62-64, pl. 6, fig. 17 (in part).

WORKER

DIAGNOSTIC CHARACTERS: Extensively yellowish red form, predominantly so on the joints of the leg above the tibiae and sometimes to the inclusion even of the joints from the tibiae downward, usually largely so (although more or less clouded, especially below) on the mesopleura, as well as on the tubercles and the sides of the propodeum. The mesonotum (except for its lateral stripe) black. The tegulae ferruginous to yellowish. The ab-

domen sometimes fuscous to chestnut colored but more often reddish, with frequently indistinct narrow yellow banding on especially tergites 2 to 5. The hairs on the under side of the abdomen pale.

HEAD: Predominantly black, but the clypeus sometimes more or less tinged with dark red and the labrum and mandibles usually cloudy dark reddish to sometimes largely black. Ferruginous are at least the base of the scape, but sometimes there is a feeble stripe from base to apex on the scape anteriorly; the antennal sockets; and the flagellum beneath (sometimes also more or less above at apex). The minute erect hairs on the clypeus and the longer erect hairs on the front and vertex black. The hairs fringing the inferior margin of the mandibles more or less yellowish, the erect hairs on the lower part of the genal area silvery gray as is the pruinescence on the upper half of the genal area, which is denser than are the silvery gray, appressed, microscopic hairs on the sides of the face and front.

THORAX: With the mesonotum black but bordered on each side by a well-developed stripe of yellow extending from a point opposite the base of the tegulae to, or virtually to, the usually triangularly maculated axillae. Almost invariably, in addition, a yellowish or reddish stripe posteriorly on the scutellum. The mesopleura sometimes almost wholly yellowish red, but almost invariably there is some clouding (more especially on the lower half) and in extreme cases the black has almost obliterated the red not only on the lower half but also on the upper half (specimens from Río Negro, Bolivia). The erect hairs on the mesonotum predominantly black but usually those in the anterolateral angles (as well as, more rarely, those along the anterior border) more or less yellowish. The hairs of the scutellum black. The hairs of the upper half of the mesopleura slightly yellowish, grading into silvery gray on the lower half; sometimes a few darker hairs just below the tegulae. The erect hairs on the sides of the propodeum that are interspersed with the silvery gray tomentum likewise silvery gray.

LEGS: With the coxae, trochanters, and femora pale bright rufo-testaceous, especially so in the case of the hind femora, but almost invariably there are coal-black contrasting maculations on the apex of the coxae, oc-

asionally on the trochanters beneath, and particularly at the apex of the femora (these black maculations are strongest in the specimens from Ivon Beni and Río Negro, Bolivia). The tibiae more variable in coloration: in Bolivian specimens from Río Negro and in occasional specimens from Cavinás and Ivon Beni black, but most specimens from the last two localities as well as from Tumupasa, Bolivia, from Hda. San Juan, Peru, and also from Pará and Igarapé-Assú, Brazil, have fore and middle tibiae that, while clouded at the apex, are on the whole only a trifle deeper in tone than the brightly colored, more basal joints. The hind tibiae usually darker than the fore and middle tibiae, at least on their apical two-thirds, but the raised area on the under side of the hind tibiae is frequently more or less reddened. The metatarsi usually black and the small joints of the tarsi also more or less darkened except for the ferruginous apical half of the claw-bearing joint. The hairs silvery gray on the coxae, on the trochanters (except the middle pair, which is apt to have partly golden hairs), and usually on the under side of the front and middle femora. The short erect hairs on upper side of hind femora usually black but sometimes pale (specimens from Tumupasa and occasional specimens from other localities). The short hairs externally on the fore and middle tibiae and the long hairs on the under side of the middle tibiae variable from dark to pale, being predominantly or wholly silvery gray in specimens from Tumupasa and in some specimens from Cavinás that have these tibiae reddish, but usually black in specimens in which these tibiae are dark. The hind tibiae fringed anteriorly and posteriorly with black hairs. The metatarsal joints externally with black hairs (those of the fore pair in rare instances with paler hairs); the metatarsal joints within golden to sometimes copper colored or black in the case of the hind pair.

WINGS: Fairly transparent, tinged with yellowish. The stigma and venation ferruginous to brownish. The tegulae ferruginous to sometimes more or less yellowish, with frequently a distinct pupil. Number of hamuli per lower wing ranges from seven to nine. Of a total of 44 wings examined, 33 had eight hamuli, six had nine hamuli, and five had seven hamuli, an average of 8.02.

ABDOMEN: Variable. Dorsally sometimes mainly "fuscous" (Smith's description) to chestnut, but more frequently a pale reddish or cloudy reddish. In the specimens of lighter abdomen there are frequently very narrow, black, down-bent, curvilinear stripes transversely across the middle region of tergites 2 to 5 or of some of these tergites. Usually, too, in specimens of darker as well as of lighter abdomen there is a very narrow yellowish stripe along the extreme apex of these tergites, sometimes also on tergite 1 and in the case of tergite 6 frequently broader. The under side of the abdomen lighter than the upper and lighter, too, than the hind femora, very pale rufo-testaceous to sometimes more or less cream colored. The erect hairs on tergites 5 and 6 black, the erect hairs on the sternites silvery gray to yellowish.

MEASUREMENTS: Length 7 to 9 mm.; width of thorax about 3 mm.; length of forewing, including tegula, about 7.75 mm.

QUEEN

See discussion of *capitata* variety *capitata* (p. 450).

MALE

See discussion that follows.

TYPE MATERIAL

The type of *femorata*, described from the Amazon region of Brazil, is in the museum at Oxford University.

DISCUSSION

While there is considerable variability among the specimens here assigned to variety *femorata*, as a perusal of the redescription offered will indicate, *femorata* is nevertheless rather distinct, even within these broad bounds, from the other varieties of *capitata*. A fuscous abdomen, such as that noted in Smith's description, is not uncharacteristic of workers from the State of Pará but is shared also by specimens from other regions. More usual is, however, an abdomen dorsally light red, with frequently very narrow pale bands apically, especially on tergites 2 to 5.

Two males before me from the State of Pará, Brazil, are hardly to be differentiated from the male of typical *capitata*. Unlike workers of variety *femorata* they have the

mesopleura black, not more or less extensively red, and the legs of at least one of the two specimens fall within the range of variability noted for the legs of the typical form, while in the case of the other male the lighter coloration may be due to a callow state. Ducke in his account of the stingless bees of Pará (1902b, p. 300) speaks of the abdomen of the male as often uniformly brown red (with the yellow maculations scarcely indicated), whereas he refers to the coloration of the abdomen of the worker as brown to blackish brown. This would seem to indicate that in the estimation of Ducke the abdomen of the male in Pará specimens is less dark than in the Pará workers, and the two males before me, which were both collected by Ducke, support this impression.

According to Ducke (1901, pp. 49, 64; 1902b, p. 300) this bee visits *Waltheria viscosissima* and *Stylosanthes angustifolia* as well as *Dichromena ciliata* Vahl in large numbers (Ducke, 1902a, p. 325).

DISTRIBUTION

The variety *femorata* was described from the Amazon region of Brazil. Specimens from the State of Pará that I have seen are assignable to this variety, which is also abundantly represented in Bolivia. From the other states the representation is sparser, there being but a single specimen before me from the Canal Zone. The localities follow:

CANAL ZONE: Alhajuela, May 28, 1912 (A. Busck).

COLOMBIA: Department of Meta: Restrepo, 500 meters, 1936 (J. Bequaert).

BRAZIL: State of Pará: Pará, April 21, 1900 (Ducke); Igarapé-Assú, June 27, 1929 (Parish).

PERU: Hda. San Juan, Colony of the Perené, June 23, 1920 (Cornell Univ. Exped.).

BOLIVIA: Tumupasa, Dec. (W. M. Mann); Río Negro, Jan. (W. M. Mann); Ivon, Río Beni, Feb. (W. M. Mann); Cavinass, Feb. (W. M. Mann).

TRIGONA SUBGENUS OXYTRIGONA COCKERELL

Trigona (Oxytrigona) COCKERELL, 1917, p. 124. *Oxytrigona*, MOURE, 1944a, p. 71.

TYPE SPECIES: *Trigona mediorufa* Cockerell.

WORKER

DIAGNOSTIC CHARACTERS: Distinguished from the other subgenera of *Trigona* by the

following combination of characters: Head notably short and wide, in the proportion of about 8 to 11, with its lower half finely and rather densely punctate to tessellate, corresponding with the presence of minute appressed hairs, but the upper half of the head, in contrast, virtually sculptureless, shiny and largely devoid of hairs, which make their appearance only as the ocelli are approached and on the vertex. Malar space very well developed. Hairs fringing the hind tibiae simple.

with the middle one only barely anterior to the lateral ones and placed in a depression, in contrast to the lateral ones, which are somewhat protruding and tilted outward. The distance between the lateral ocelli hardly less than the distance separating each of these ocelli from the compound eye. A feeble carina behind the ocelli and about coëxtensive with them. The clypeus very widely separated from the compound eye (the distance is about three times that of the width of the flagel-

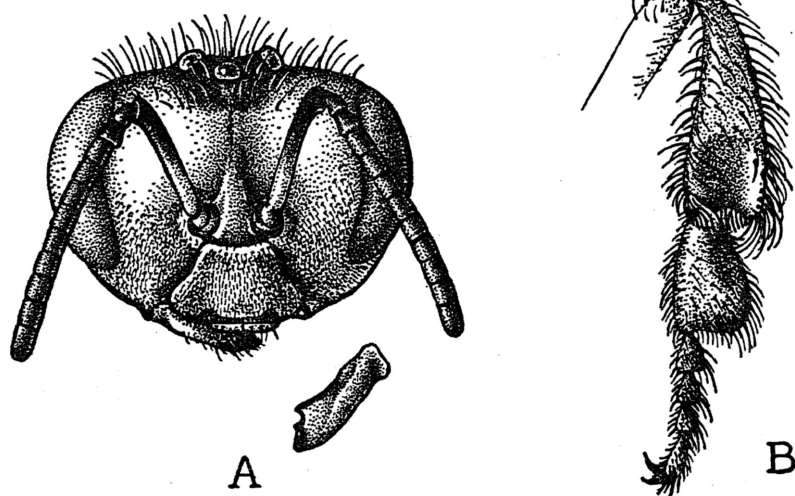


FIG. 76. Worker of *Trigona* (*Oxytrigona*) *tataira* variety *tataira* F. Smith. A. Head and mandible. B. Tibia and tarsal joints of hind leg. Drawings by Shirley H. Risser.

HEAD (FIG. 76A): Rather disproportionately short compared to its width, which is somewhat greater than the distance between the outer rims of the tegulae. The facial quadrangle wide, the distance between the compound eyes at the level just below the anterior ocellus about equal to the distance from the anterior ocellus to the apex of the clypeus. (This comparison is based on the measurements arrived at on a reticulated scale, which, however, cannot take account of the receding front, apparent only when the insect is viewed in profile; if allowance is made for this recession, the distance between the middle ocellus and the apex of the clypeus is notably increased.) The eyes convergent below, short and rather narrow, only a little more than one-half the width of the genal area. The ocelli arranged almost linearly,

lum), not notably raised above the level of the sides of the face but of slightly undulating surface, with often a faint bulge on each side of the middle or covering the entire middle. The height of the clypeus compared to its width is about as 2.75 is to 4.25, or about three-fifths; its oblique sides are gradually and at no point abruptly divergent, its antero-lateral angles slightly rounded, its apex widely truncate with a short recession at each of its extremities. The sugarloaf-shaped supraclypeus rather more prominent than the clypeus. The length of the malar space fully twice the width of the flagellum. The labrum simple. The mandibles overlapping, slightly hourglass shaped, their apex smooth on its outer two-thirds but with two denticles on the inner one-third. The clypeus and the area between the clypeus and the compound

eye to the level of the antennal socket slightly dulled by fine, rather dense punctation to tessellation, but the upper half of the head and the genal area on the whole smooth and shiny. Very few erect hairs on the head, these being confined to the extreme upper part of the front, the vertex, far inward towards the lower extremity of the genal area, fringing the mandibles below, and on the labrum. Ultra-minute, microscopic, appressed hairs are present in the sculptured area on the lower half of the head. The scape slightly more slender than the flagellum and about one-half as long, devoid or virtually devoid of hairs.

THORAX: With the greatest width of the mesonotum (at the base) about equal to the length of the mesonotum and scutellum combined. The scutellum rounded posteriorly, not in the least protuberant, failing to over-roof in the slightest the somewhat longer, down-sloping propodeum. The thorax sculptureless and smooth, rather densely covered with hairs, but the middle area of the propodeum hairless and very shiny. The hairs longest on the scutellum and towards the under side of the thorax; more or less tomentose, in addition to simple hairs, on each side of the bare middle area of the propodeum.

LEGS: Progressively longer from front pair to hind pair, the long hind leg being about as extensive as the combined length of the head, thorax, and abdomen. The hind tibia (fig. 76B) about equal to the combined length of the hind femur and trochanter, its shape clavate to subtriangular with the apex bearing a tiny angulation anteriorly (to which is attached the comb), an emphatic angulation posteriorly and a rounded contour between that separates the two angulations. The outer face of the hind tibiae flat to slightly arched on its basal two-thirds but with a depression on the apical one-third. The under side of the hind tibia with a slightly raised area that is covered densely with microscopic, silvery gray hairs and that contrasts with the sharply declivitous area (with longer hairs) anterior to it and the narrow flat hind rim. The hind metatarsus wide, at its widest fully two-thirds as wide as the hind tibia at its widest, thickened anteriorly, more pinched behind, posterior contour convex and rapidly receding inward on the basal half. The hairs fairly

abundant, being present on the coxae, under side of trochanters, under side and outer side of fore and middle femora and also on upper side but reduced in size; those on outer side of hind femora distinctly longer than those on inner side of these femora. Hairs abundant on fore and middle tibiae both externally and within, but longer on the inner side of the middle tibiae than on the inner side of the fore tibiae, although the hairs growing posteriorly on the fore tibiae tend to be long. The hairs on the inner side of the middle tibiae are also decidedly longer than those on the outer side of these tibiae. The hind tibiae, fringed anteriorly and posteriorly with simple, eyelash-like hairs, bear on their outer face a few additional erect hairs. The hairs on the outer face of the fore and middle metatarsi longer than those of the brushes on the inner face. The hairs along the anterior lateral contour of the hind metatarsi denser but not quite so long as those along the posterior lateral contour; within, this joint is covered with bristles from base to apex.

WINGS: With the transverse cubital veins usually only feebly indicated to absent except in the case of the upper half of the first transverse cubital, which is usually (not always) clearly indicated. The first discoidal cell about nine-tenths as long as the marginal cell. The number of hamuli per lower wing usually six or seven but with a range of from five to eight.

ABDOMEN: At the base a little narrower than the thorax, arched ventrally as well as dorsally. Tergite 1 polished. Tergites 2 to 6 polished basally but very finely tessellated along their apex (corresponding with the presence in this area of hairs). The tessellated area very narrow and inconspicuous on tergite 2 and the hairs few and short; the succeeding tergites with the roughened apical area larger and with progressively longer hairs. The sternites with erect hairs along the apex of each.

MEASUREMENTS: Length 4 to 6.5 mm.; width of thorax 1.5 to 2 mm.; length of forewing, including tegula, 5 to 5.5 mm.

QUEEN (GRAVID)

HEAD (FIG. 77A): Relatively smaller than that of the worker, wider than the mesonotum but not so wide as the distance from the

outer rim of one tegula to the outer rim of the other tegula. The contrast between the sculpturing of the lower half of the face and the upper possibly a little less marked than in the worker or the male, the tessellation on clypeus and adjacent parts of sides of face being light. The facial quadrangle wide, somewhat wider than the distance from the middle ocellus to the apex of the clypeus, in the

its upper margin. The malar space also very long, only a little less than the distance between the apico-lateral angle of the clypeus and the eye. The eyes slightly convergent below, very short and narrow, only about five-sixths as long as those of the worker and comparable in length with the maximum width of the clypeus. The labrum simple. The mandibles (fig. 77A) edentate along their

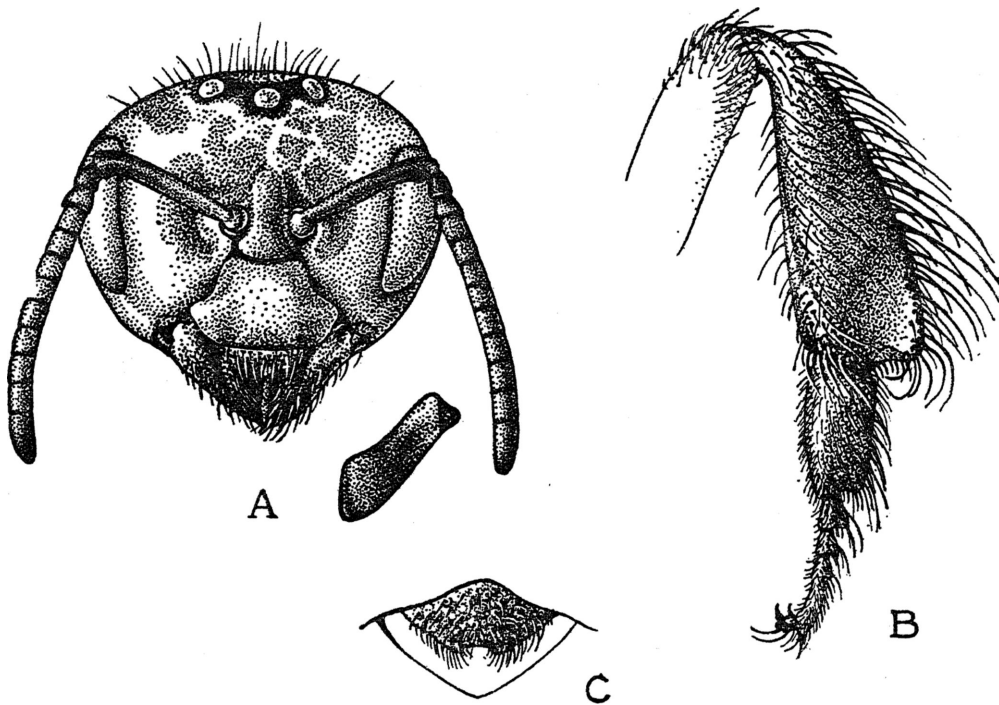


FIG. 77. Queen of *Trigona* (*Oxytrigona*) *tataira* variety *tataira* F. Smith. A. Head and mandible. B. Tibia and tarsal joints of hind leg. C. The last visible sternite of the abdomen, seen against tergite 6 in outline. Drawings by Shirley H. Risser.

proportion of about 8.5 to 8. The clypeus slightly raised above the level of the sides of the face; the supraclypeus a little more prominent than the clypeus and about twice as high as its width below. The clypeus about three-fifths as long as its greatest width, of irregular surface, a little more elevated in the middle region. The apex of the clypeus truncate along its middle but sharply receding at each extremity; the apico-lateral angles formed by these recessions at their junction with the sides of the clypeus very remote from the eye, the intervening distance being about equal to the width of the clypeus along

entire apical edge. The ocelli arranged in a very obtuse triangle with the middle one in a depression and only slightly anterior to the somewhat outward-tilted lateral ocelli. The lateral ocelli separated from the middle ocellus each by about the diameter of an ocellus. The ocelli as a group very remote from eye. Measured from the outer rim of a lateral ocellus, the distance to the eye is about one and one-half times the distance that separates the lateral ocelli from each other. A blunt carina behind the ocelli. The flagellum about twice as long as the scape. The head with as little hair as that of the worker. The clypeus,

sides of face, and front bare as is the genal area except for a very few short hairs at the lower extremity. A few hairs on the vertex, on the labrum, and fringing the mandibles below. The scape devoid of hairs.

THORAX: Short, the combined length of the mesonotum and scutellum being subequal to the greatest width of the mesonotum, which is emphatically wider than the mesonotum of the worker. The scutellum short, rounded posteriorly, not in the least over-roofing the somewhat longer, down-sloping propodeum. The thorax smooth but its sheen subdued owing to the presence of many hairs. These are appressed or semi-appressed on the mesonotum except for a few erect hairs for the most part near the anterior border. Particularly long and conspicuous are the bristles on the scutellum, especially those fringing the scutellum posteriorly, which are about as long as the scutellum itself. The hairs on the mesopleura erect and rather dense and a few erect hairs also among the mainly appressed hairs on each side of the bare middle area of the propodeum.

LEGS: More robust and with longer hairs than those of the worker. The middle legs intermediate in length between the short fore legs and the long hind legs. The fore and middle tibiae distinctly shorter than their respective femora, reversing the condition of the hind pair of legs, in which the tibiae are longer than the femora although distinctly shorter than the combined length of the trochanters and femora. The hind tibiae (fig. 77B) wider than those of the worker by about one-third and also longer; somewhat clavate in outline but with the base relatively wider when compared to the apex than is the case in the worker. The apex of the hind tibiae much as in the worker, with a tiny anterior angle (easily overlooked), followed by a rotundity in the contour and in turn succeeded by the posterior angle, which is less emphatic than it tends to be in the worker. The outer face of the hind tibiae rather arched anteriorly but with a depression posteriorly in the apical one-third. The under side of the hind tibiae with a slightly raised area (covered densely with short bristles) that contrasts with the narrow flat rim that borders it posteriorly. The hind metatarsi about one-half as wide as the hind tibiae and

about as long as the small joints of the hind tarsi combined; the width of the hind metatarsi at the base about one-half their length and a little greater than their width at the apex. The hairs on the hind coxae, at least, fairly long, longer than the fine hairs on the under side of the trochanters, including those on the trochanters of the middle pair. The fore and middle femora with relatively fewer hairs than the corresponding joints in the worker and these hairs mostly on the under side; the hind femora with hairs on their outer face that become longer and rather coarse at the apex. The fore and middle tibiae both externally and within very much more hairy than the femora. The long hairs posteriorly on the fore tibiae subequal to the hairs on the outer face of the fore metatarsi but much shorter than the still longer hairs posteriorly on the middle tibiae. A fringe of short simple hairs on the anterior contour of the hind tibiae and a fringe of similar but much longer hairs on the posterior contour, a few of these hairs being as long as the joint is wide. Erect to semi-erect hairs of somewhat irregular length scattered over the outer face of the hind tibiae. The dense brushes on the inner side of the metatarsal joints composed of hairs that are shorter than the sparser hairs on the outer side of these joints. The tarsi of the hind leg with a fringe of rather long hairs along their posterior lateral contour.

WINGS: Approximately of the same length as those of the worker.¹ The upper half of the first transverse cubital vein strongly chitinated.

ABDOMEN: Much distended, with the result that it is both wider and deeper than the thorax and longer than the combined length of head and thorax. Tergite 1 smooth and shiny but with traces here and there of scattered fine punctation; tergites 2 to 4 also shiny but with punctation that is much more apparent, even fairly dense on tergites 3 and 4. Unlike the worker in these respects, the queen is also unlike the worker in that it has no apical hair bands on these tergites. There

¹ The wings in the only specimens available are badly frayed, making measurement difficult. Only two hamuli are traceable in each hind wing, but probably others were broken off in the fragmentation of the wings, so that this low number of hamuli is not representative.

is, however, a rather large, silvery gray, sericeous patch at each side of the base of tergite 3 and a smaller patch similarly located on tergite 4. Tergites 5 and 6 with hairs over all their exposed surface, the hairs on tergite 6 consisting of appressed as well as of fairly long erect hairs. The apices of the sternites, at least towards their middle, with erect hairs. The last visible sternite (fig. 77C) feebly emarginate at the apex and covered with moderately long erect hairs.

as 2.75 is to 3.5, or approximately four-fifths; its sides obliquely divergent from base to apex, its apex truncate along the middle but sharply recessive at each extremity. The supraclypeus a little more prominent than the clypeus, sugarloaf-shaped, about twice as high as it is wide below. The malar space about as long as the scape is wide. The labrum simple. The mandibles, when retracted, only very slightly overlapping; their apex, not much narrower than their base, is often

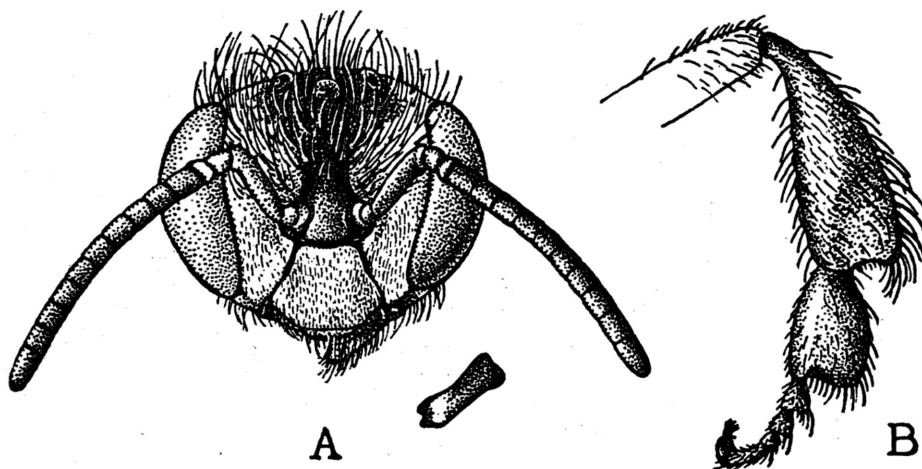


FIG. 78. Male of *Trigona* (*Oxytrigona*) *tataira* variety *tataira* F. Smith. A. Head and mandible. B. Tibia and tarsal joints of hind leg. Drawings by Shirley H. Risser.

MEASUREMENTS: Length 8 mm. (abdomen 4.5 mm.); width of thorax 2.5 mm.; length of wing (estimated) about 5.25 mm.

MALE

HEAD (FIG. 78A): Rather disproportionately short compared to its width, which is somewhat greater than the distance between the outer rims of the tegulae. The eyes strongly convergent below, larger than in the worker, about as wide as genal area. The facial quadrangle much narrower than in the worker, and much narrower below than above, the distance between the eyes near their summit and the distance separating the eyes at their level of closest approximation below being in about the proportion of 6.5 to 5. The clypeus separated from the compound eye by fully the width of the flagellum, not notably raised above the level of the sides of the face; its height compared to its width is about

feebly bidentate (fig. 78A), but in other cases the denticles are not traceable. The ocelli arranged almost linearly, with the median ocellus in a depression, only slightly anterior to the lateral ones, which are tilted outward. Each lateral ocellus separated from the nearest compound eye by about double its own diameter. A blunt low carina extending behind the ocelli. The clypeus and the area between the clypeus and the compound eye to, or somewhat beyond, the level of the antennal sockets slightly dulled by fine rather dense punctation to tessellation. The upper half of the head usually with only a few feeble traces of sculpturing, largely smooth and shiny, as is the genal area. Ultra-minute, microscopic, appressed hairs may be traced only with difficulty in the sculptured area on the lower half of the head. The erect hairs of the upper part of the head more abundant and longer than in the worker, not confined

to the vertex and the extreme upper part of the front (as in the worker) but extending down to the level of the upper end of the supraclypeus. There are also fairly long hairs inwardly towards the lower end of the genal area and a fringe along the lower margin of the mandible that includes hairs sometimes twice as long as the mandible is wide at the base. The flagellum slightly wider than all but the apical part of the scape and nearly four times as long as the scape. The scape devoid or virtually devoid of hairs.

THORAX: Smooth and shiny; the greatest width of the mesonotum (at the base) barely less than the length of the mesonotum and of the scutellum combined. The scutellum rounded posteriorly, not in the least protuberant, failing to over-roof in the least the slightly longer, down-sloping propodeum. The hairs abundant over all the areas except the bare middle area of the propodeum. The hairs are long and erect on the mesonotum and mesopleura but even longer on the scutellum, which they equal in length.

LEGS: Progressively longer from front pair to hind pair, the long hind leg nearly comparable in length with the other body parts combined. The legs on the whole smooth, but tessellated in the following areas: outer face of middle tibiae (somewhat), outer face of hind femora (especially towards apex), outer face of hind tibiae (especially anteriorly), inner face of hind tibiae, outer face of hind metatarsi. The combined tarsal joints of the middle legs about equal in length to the combined tarsal joints of the hind legs. The hind tibiae (fig. 78B) in outline very similar to those of the worker, clavate, with the apical contour rounded anteriorly and rather strongly angulate posteriorly, but much more thickened (although a shade narrower) than those of the worker. The hind metatarsi also more thickened than those of the worker, about as long as the following tarsal joints combined, the width of the hind metatarsi slightly more than two-thirds that of the hind tibiae at their widest, their posterior contour convex, their apical contour broadly rounded posteriorly. The hairs a little longer on the under side of the hind coxae than on the under side of the anterior, middle, or hind trochanters, but they are still longer posteriorly on hind coxae. The hairs basally on

under side of fore and middle femora fairly long but diminish in size towards the apex of these joints; short hairs on the upper side of the femora, especially in the case of the middle pair; the hind femora with rather numerous hairs on the outer side and also above but with only rather minute and inconspicuous hairs on their inner side and beneath. The outer face of the fore and middle tibiae with a few hairs but with a posterior fringe of longer hairs and, in the case of the middle tibiae, with longer hairs also on the under side. The hind tibiae with semi-erect hairs over their outer surface and a fringe of simple hairs along the anterior as well as the posterior contour, the hairs of the posterior contour a little the longer. The under side of the hind tibiae with silvery gray microscopic hairs. The hairs on the outer face of the fore metatarsi and those of the posterior fringe sparser but longer than those of the brush on the inner face. The hairs on the outer face of the middle metatarsi and those of the posterior fringe sparser but nearly of the same length as those of the brush within. The hairs on the outer face of the hind metatarsi short and inconspicuous, but posteriorly on this joint there is a thin fringe of hairs about the same length as those of the brush on the reverse side.

WINGS: Similar to those of the worker. The number of hamuli per lower wing ranges from four to seven, but four is a rarity.

ABDOMEN: At the base a little narrower than the thorax, arched dorsally and also at the base ventrally but with the sternites towards the apex tending to be medianly more or less concave. The tergites for the most part polished and shiny but with an apical border of very fine tessellation. This border narrow on tergites 2 to 4, a little wider on tergites 5 and 6, and the hairs on the tessellated area of tergites 5 and 6 longer than the very inconspicuous hairs in the corresponding areas of tergites 2 to 4. The apex of the dorsal side of the abdomen with a rather dense fringe. The ventral side sericeous, more densely so on sternites 3 to 5. For the structure of the sternites and genitalia, see figure 79.

MEASUREMENTS: Length 4.5 to 6.75 mm.; width of thorax about 1.75 mm.; length of forewing, including tegula, about 5.25 mm.

DISCUSSION

Cockerell (1917, p. 124) erected the subgenus *Oxytrigona* with the following comment: "These bees of the 'coccofago' group, with their very broad heads and remarkable habits, may be regarded as a distinct subgenus (*Oxytrigona* subg. n.)." Cockerell hesitated between considering the several forms that constitute this genus as independent species or as "races of an aggregate species" but in

to their aggressiveness rely upon a scalding fluid which they discharge upon those whom they attack. The popular names applied to these bees are indicative of their unsavory reputation. A common name is "cacafogo" or "cagafogo," variously translated as excrement of fire (A. de Saint-Hilaire, 1830, p. 374), spit-fire (H. Müller, 1874, p. 32), and fire-defecator (Wheeler, 1913, p. 8). The other widely applied name is "tataira," which is of

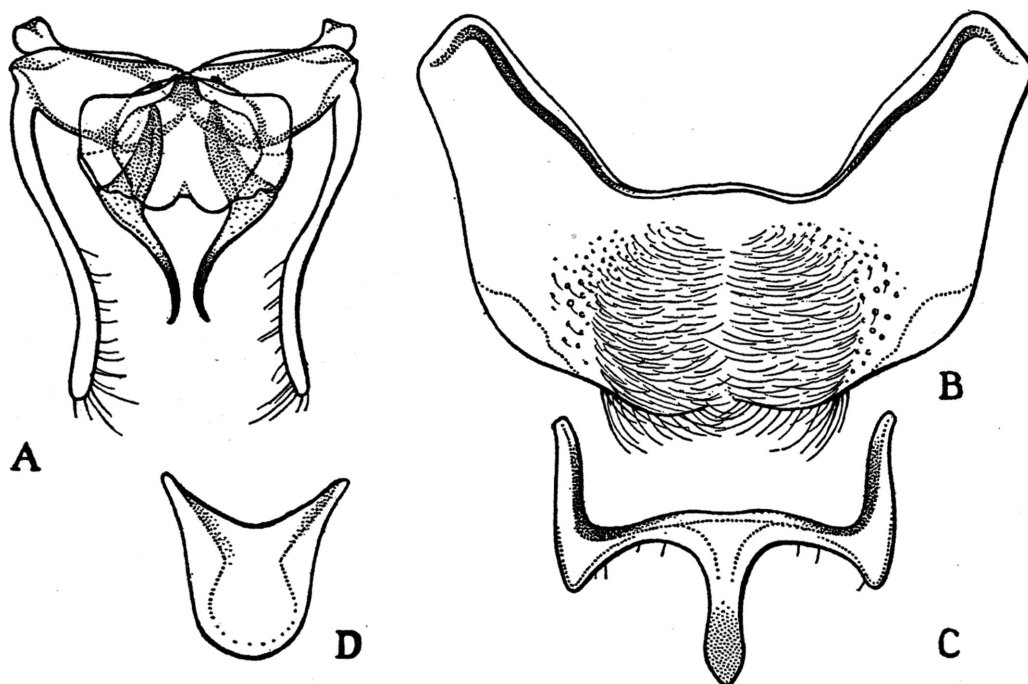


FIG. 79. Abdominal parts of male of *Trigona* (*Oxytrigona*) *tataira* variety *mellicolor* Packard. A. Genitalia (chitinized parts only). B. Sternite 5. C. Sternite 6. D. Sternite 7. All based on a specimen from Volcan de Chiriqui, Panama. Drawings by Shirley H. Risser.

any event regarded *mellicolor* Packard as distinct. In the present paper all of the forms, to the inclusion of *mellicolor*, are made varieties of *tataira*.

Moure (1944a, p. 71) elevated *Oxytrigona* to the rank of genus, but I personally should prefer to consider it, like certain other subgenera of stingless bees that in the same paper were elevated to generic rank, as more aptly classified as a subgenus.

Deprived as they are of an effective sting, most *Trigona* lack adequate weapons of defense other than their mandibles, but members of the subgenus *Oxytrigona* in addition

indigenous origin. Bertoni (1911, p. 144) indicated that the syllable "tata" means fire and that the name in the Guarini language for the bee is "eira-tata" by virtue of the irritation it causes the skin. Thus the names "tataira" and "cacafogo" would both seem to emphasize the caustic character of the fluid discharged. On the other hand, Saint-Hilaire (1830, p. 374) derived the name "tataira" from "tatura," meaning red, a reference to the prevailing coloration of the insect.

Writers who have encountered these bees are in agreement as to their viciousness and

the unpleasant after-effects of their attack. A very early reference is that of Coelho de Scabra (1799, pp. 101, 103), who indicated that the caustic fluid was, as it seemed, ejected from the anus. Some 30 years later Spix and Martius (1828, p. 542) erroneously attributed the serious inflammation caused by "caca-fogo" to a sting rather than to the discharged fluid. Saint-Hilaire (1830, p. 372), on the other hand, was aware of the fact that the bees are stingless and, like Coelho de Scabra, spoke of their discharging the scalding fluid from their anus. This is the opinion, too, of Peckolt (1893, p. 580), who definitely asserts that an anal gland secretes the poison (1894, p. 225). Saint-Hilaire as well as Spix and Martius indicated that, because of the irritating habit of these bees, it was only at night time that attempts were made to deprive them of their honey. The bee's singular means of defense, wrote H. Müller (1874, p. 32), "are indicated by the vernacular name Cagafogo (spit-fire), for although stingless, like all other Trigonas and Meliponas, it possesses a very intense venom, which causes a most lively irritation in the skin. Whilst the defenseless species are for the most part very peaceable, the Cagafogos, on the contrary, are so irritable that the observation of their nests proves impossible, unless cold weather or strong breezes from the land keep them quiet."

Hermann von Ihering (1903, p. 206) offered this theory as to how the "cagafogos" poisoned their victims: "As I have not observed the bee alive, I can not speak regarding it with precision, but I infer from the description that the bee makes a small incision in the skin by nipping with its mandibles and then squirts into the wound the secretion of its poison glands. There results a red spot about 1 mm. in diameter the epidermis of which is lacking; the small wound is usually not entirely healed until after the elapse of one to two weeks." Silvestri (1902b, pp. 144-145) thought the irritating fluid was injected in the act of biting, which seems also to have been the opinion of Drory (1873a, p. xxxii; 1877, pp. 147-148), Raveret-Wattel (1875, p. 739), Girard (1876a, p. 194), Holmberg (1887, p. 260), and Phisalix (1922, p. 429). Silvestri was attacked when approaching a nest in a dead tree trunk near the

Rio Cuyabá and was bitten in various parts of his head, with a resultant slight burning sensation. "The burning sensation of the bite," Silvestri concluded, "is due to the nature of the saliva, which seems to contain a great deal of formic acid; at any rate, the odor reminded me strongly of that substance." Bertoni, too (1911, p. 144), believed the poison of these bees to be formic acid. Marianno (1911, p. 85) was of the opinion that the irritating liquid proceeded from the salivary glands and was regularly present at the tip of the mandibles whenever the insects made their attacks.

From these interpretations there is dissent by Wheeler (1913, pp. 8-9), who was severely mauled by *Oxytrigona* in Guatemala. "One is, of course, hardly in a proper frame of mind during an assault of these terrible bees," stated Wheeler, "to make accurate observations on the source of their caustic secretions. I am convinced, nevertheless, that the liquid comes from the poison (anal) glands and not from the mouth as Silvestri supposes, because the odor is precisely like that of the poison glands of the Dolichoderine ants (*Tapinoma*, *Azteca*, *Liometopum*, etc.) and of some other insects with anal glands (Carabidae). The secretion is not, however, applied in the manner described by von Ihering, because the bees did not make small holes in my epidermis, but simply spread the liquid over it in considerable quantity, so that the surface was quite wet. Hence, after the attack, the cuticle was not reddened in definite small patches but was diffusely flushed over larger areas as in the case of sun-burn."

The spots, "which the bees had moistened, remained sensitive and painful to the touch for several days and in the course of the next two weeks lost their epidermis as if violently sunburned." In these words Wheeler (1913, p. 8) graphically described the reactions he experienced. According to Drory (1873a, p. xxxii) a victim of these bees in Bahia, Brazil, bore the evidences of their attack for more than three weeks, while in his own case the scars of battle were visible for more than four months (Drory, 1877, p. 148). On the other hand, Holmberg (1887, p. 260), summarizing the field experiences of Lucchesi and Goicochea, indicated that, following an attack, there would be painful effects for three or

four days, and incapacity to work for eight days. Evidently the effects depend on the strength of the attacks and the condition of the individual victimized or both, and indeed Coelho de Scabra, writing nearly a century and a half ago (1799, p. 103), spoke of the caustic fluid discharged by "caga-fogo" as being "a more or less active stimulant."

In addition to the irritation of the skin, those attacked by bees of this subgenus suffer, according to Marianno (1911, p. 85), accompanying discomforts of vomiting, fever, and headache. Drory (1877, pp. 147-148) found the odor of the emissions of *Oxytrigona* bees so overpoweringly revolting that "if you have a dozen or two in your moustache, you risk having an attack of dizziness or an upset stomach." Evidence to the same effect if less picturesquely stated is contained in an earlier account of Drory (1874, p. 285).

In view of the menacing behavior of members of the subgenus *Oxytrigona* it is not surprising that their nests are better known from the outside than from within. In nearly all of the cases reported, the nest site has been a hollow space within a tree (see especially the discussion of typical *tataira*). However, Peckolt (1894, p. 225) saw a nest that had been built among the roots of an epiphyte. The nest itself may be variable. The external architecture, at any rate, does not seem to be standardized. H. Müller (1874, p. 32) did not allude to a protruding entrance tube, which prompts the belief that the two nests of *tataira* that he observed lacked this structural feature. Bertoni (1911, p. 144) indicated that such a tube is not provided, and Wheeler (1913, p. 8) confirmed its absence also in the case of a nest of variety *mediorufa*. H. von Ihering (1903, p. 206) spoke of the flight tube of *tataira* as small and insignificant. In contrast seemingly to these statements regarding the small size of the tube or, more often, its complete absence, is the statement of Marianno (1911, p. 85) who reported that nests of *tataira*, referred to as *cagafogo*, have an external formation of wax, 4 to 9 cm. in height and 5 to 7 cm. in width, in whose center is a vertical crevice 4 to 6 cm. in height by 5 to 7 mm. in width. Sometimes the upper extremity of the crevice is bifurcated, giving forth two divergent branches. In such cases, which occur rather

frequently, the crevice takes the form of a Y.

In the internal structure, too, there seems to be possibly some diversity of building technique. The brood combs are horizontally placed but in none of the brief earlier descriptions of nests (H. Müller, 1874, p. 32; Bertoni, 1911, p. 144) is there indication that any part of the nest architecture is spiral. Yet such seems to have been the arrangement of the combs in a nest of variety *mellicolor* regarding which the late F. Nevermann wrote me, unfortunately all too briefly.

KEY TO THE VARIETIES OF *Trigona* (*Oxytrigona*)

WORKERS

1. At least the middle and hind legs exclusively or almost exclusively black or reddish brown, without or virtually without fulvous or orange ferruginous maculations 2
The middle and hind legs either without black or with at least their coxae, trochanters, and femora above wholly or almost wholly fulvous to orange ferruginous; the fore legs usually without black except sometimes on the metatarsi and rarely also on the tibiae and on the femora beneath 4
2. The hairs fulvous, or for the most part fulvous, on vertex, mesonotum, mesopleura, scutellum, and abdominal sternites. The mesonotum with its median one-third (widened posteriorly) orange ferruginous. The fore wings hyaline to more or less milky, with the median cell sometimes faintly orange tinted and the neuration and stigma honey colored *tataira* variety *mediorufa* Cockerell
The hairs black on the vertex, mesonotum, mesopleura, scutellum, apical abdominal tergites, and abdominal sternites. The mesonotum usually uniformly black, rarely with the median one-third contrastingly reddish. The forewings as a rule darkened at least in the median and marginal cells; the stronger nervures brown to blackish. (In rare instances the wing lacks these dark areas and the venation and stigma in such cases may be honey colored) 3
3. The head reddish yellow to orange ferruginous, with usually a black area between and below the ocelli. The mesonotum usually black, rarely (callows?) with its median one-third red. The axillae and the scutellum usually reddish. The abdomen reddish
. *tataira* variety *tataira* Smith
The upper part of the head completely black, the genal area black or reddish black; the

lower half of the face contrastingly pale. The mesonotum black; the axillae black; the scutellum usually black, sometimes invaded by reddish black. The abdomen black or reddish black.

- *tataira* variety *obscura* Friese
4. The median and marginal cells and a narrow area immediately below the apical half of the marginal cell smoky; the venation and stigma brown
- *tataira* variety *mulfordi*, new variety
- The median cell sometimes faintly orange colored but not smoky; the marginal cell, like the other cells, subhyaline; the venation and stigma bright ferruginous or honey colored 5
5. The legs exclusively, or almost exclusively, fulvous to orange ferruginous. Bare area of propodeum black or blackish, occasionally some of the abdominal tergites clouded
- *tataira* variety *mellicolor* Packard
- The legs with more or less black; at least the middle and hind metatarsi and the greater part or all of the hind tibiae blackened. Bare median area of propodeum not at all or barely darkened
- *tataira* variety *flaveola* Friese

QUEENS AND MALES

(No key is offered for the queens or the males of *Oxytrigona* because of the inadequacy of our knowledge regarding these castes in the different varieties of *tataira*.)

Trigona (Oxytrigona) tataira variety *tataira* F. Smith

- "Caga-fogo," COELHO DE SCABRA, 1799, pp. 101, 103.
- "Tata hira," HENDERSON, 1821, p. 508.
- "Caca-Fogo," SPIX AND MARTIUS, 1828, p. 542.
- "Tataira," SPIX AND MARTIUS, 1828, p. 542.
- "Tataira," SAINT-HILAIRE, 1830, pp. 373, 374.
- "Caga fogo," SAINT-HILAIRE, 1830, pp. 373, 374.
- "Tata hyra," PERTY, [1833], p. 28.
- "Caca-fogo," PERTY, [1833], p. 28.
- ? "Tataira," ACKERMANN, 1834, p. 81.
- ? "Tataira," GARDNER, 1846, pp. 327, 328.
- ? "Tataira," GARDNER, 1849, p. 249.
- Trigona tataira* F. SMITH, 1863a, pp. 499, 508, pl. 20, fig. 7.
- "A Brazilian species of honey-bees," H. MÜLLER, 1873, pp. 201-202.
- Trigona cacafogo* and *Trigona cagafogo* H. MÜLLER, 1874, pp. 31-32, figs. 1-4.
- Melipona Cagafogo*, H. MÜLLER, 1875b, pp. 43, 48.

"Tataira" or "Tatara," RAVERET-WATTEL, 1875, pp. 737, 738.

"Caga-fogo," ANONYMOUS, 1878a, p. 73.

"Tataira preta," ANONYMOUS, 1878b, p. 74.

"Tataira," GRONEN, 1881a, p. 54.

"Eirá-tatá," HOLMBERG, 1887, pp. 260-261, 287.

Melipona tataira, PECKOLT, 1893, p. 580.

Melipona tataira, PECKOLT, 1894, p. 223.

Melipona caga-fogo, PECKOLT, 1894, p. 233.

"Caga fogo" or "Eirá tatá," AMBROSETTI, 1895, p. 699.

Trigona cacafogo, H. VON IHERING, 1903, pp. 206-207, 261, 263, 277.

Trigona cagafogo, H. VON IHERING, 1904b, pp. 381, 386.

Trigona tataira, DUCKE, 1907, pp. 75, 89.

Trigona tataira, DUCKE, 1910a, p. 109.

Trigona tataira, DUCKE, 1910b, p. 367.

Trigona cacafogo, MARIANNO, 1910d, pp. 8, 10.

Trigona coccofago, STRAND, 1910, p. 559.

Trigona tataira, BERTONI, 1911, pp. 139, 144.

Trigona cagafogo, MARIANNO, 1911, pp. 22, 25, 32, 51, 53, 84, 85.

Melipona tataira, DUCKE, 1916, p. 26, opposite p. 28, pp. 30, 42-44.

Trigona (Oxytrigona) tataira, COCKERELL, 1917, p. 124.

Trigona caccofogo, LUTZ, 1924a, pp. 205, 207, 210, 214, 220.

Melipona tataira, DUCKE, 1925, pp. 341, 342, 349, 369-370.

"Cacafogo," BOUVIER, 1926, p. 39.

Trigona cagafogo, SALT, 1929, p. 461.

Melipona tataira, GUENTHER, 1931, p. 376.

Trigona tataira, SCHWARZ, 1932a, p. 253.

Trigona cagafogo, R. VON IHERING, 1940, pp. 63, 187-188, 880.

Trigona (Oxytrigona) tataira, MOURE, 1944b, p. 2.

Melipona tataira, DUCKE, 1945, p. 23, opposite p. 24, pp. 26, 35-37.

WORKER

DIAGNOSTIC CHARACTERS: Head predominantly reddish yellow to orange ferruginous. Mesonotum (in fully mature specimens) black; axillae and scutellum reddish. Legs predominantly black or dark brown. Wings somewhat darkened over basal half, subhyaline apically. Abdomen reddish. Hairs of body and legs predominantly black.

HEAD (FIG. 76A): Reddish yellow to orange ferruginous, including usually at least the basal part of the scape and more rarely the under side of the flagellum. The upper half of

the scape usually black, especially posteriorly, and the upper side of the flagellum (and frequently the entire flagellum) also black. A solid area of irregular contour, usually in and about and particularly below the ocelli, likewise black, as are sometimes the labrum, frequently the mandibles except for their more reddish apex, and often a narrow line along the apex of the clypeus. The hairs of the vertex, labrum, and mandibles below black or blackish.

THORAX: Usually black except for the scutellum and also the axillae, which tend to be reddish, but in exceptional cases (probably callows) with the middle one-third of the mesonotum also reddish. The hairs of the mesonotum, mesopleura, and scutellum blackish, and the erect hairs among the dull gray pubescence on each side of the bare shiny area of the propodeum likewise blackish. The propodeum dark.

LEGS: Black, sometimes more or less brownish, with almost exclusively black hairs; the raised surface on the under side of the hind tibiae silvered over with microscopic hairs. (Fig. 76B.)

WINGS: Darkened on their basal half, usually a little more strongly so in the median cell than in the adjacent cells; the marginal cell also sometimes darkened but the other parts of the apical half of the wing subhyaline. The stronger nervures brown, the feebler ones dull ferruginous. (This is the usual condition; very exceptionally the forewing is hyaline to slightly milky, with the median cell orange tinted; the stigma and veins light orange.) The tegulae usually brownish, barely paler than the brown venation, but sometimes lighter, and rarely bright ferruginous (specimen from Bahia). Number of hamuli per lower wing ranges usually from six to seven, although exceptionally there may be as few as five or as many as eight hamuli. Of 75 wings counted, 38 had six hamuli, 33 had seven hamuli, three had five hamuli, and one had eight hamuli, an average of 6.43.

ABDOMEN: Reddish, with the hairs of both the tergites and the sternites black.

MEASUREMENTS: Length 4.75 to 6.5 mm. (specimen with abdomen much distended); width of thorax 1.75 mm.; length of forewing, including tegulae, about 5.25 mm.

QUEEN (GRAVID)

HEAD (FIG. 77A): Reddish yellow, more reddish over front and vertex, more yellowish on clypeus and along the inner orbits of the eyes. The upper part of the scape darkened, particularly posteriorly, and the flagellum somewhat darkened above. Interocellar blackening but the dark area not extended downward on the front as in the worker or even more emphatically in the male. The labrum yellowish. The mandibles yellowish at the base, reddish towards the apex, with an intermediate band of black on the apical half just beyond the middle. The eyes black, somewhat mottled. The hairs on the vertex, labrum, and lower edge of mandibles reddish.

THORAX: For the most part black as is the propodeum, but not only are the scutellum and axillae red but an area of black on each side, roughly one-third of the dorsal face of the thorax, is islanded and separated from the median area of black by a red stripe that runs along the full length of the lateral margin of the mesonotum, bends inward along the anterior margin for one-third of the width of the mesonotum, and then extends backward to the axillae. The resulting rather loop-like maculations are united with each other by a red stripe running along the posterior border of the mesonotum. The hairs of the mesonotum predominantly pale; those of the scutellum brownish; those of the mesopleura black but grading into pale on the under side of the thorax.

LEGS: Black to reddish brown (this lighter coloration predominant on the hind pair). The coxae and trochanters beneath of all the legs with pale hairs. The tibiae and tarsal joints externally mostly with black or blackish hairs; the inner face of the hind tibiae with pale hairs; the metatarsal brushes reddish golden. (Fig. 77B.)

WINGS: Darkened in basal half and in marginal cell, with the neurulation brown. Apical part of wing, presumably subhyaline as in the worker and male, is tattered in the individual before me.¹ Tegulae red.

ABDOMEN: Reddish, with some clouding. Hairs pale to reddish for the most part both

¹ The hind wings, too, were mutilated, making a trustworthy count of the hamuli impossible. H. Müller (1874, p. 31) implied that the coloration of the wings is the same in all the castes.

on the apical tergites and ventrally, with very few darker hairs. The last visible sternite of the abdomen is shown in figure 77C.

MEASUREMENTS: Length 8 mm. (abdomen 4.5 mm.); width of thorax 2.5 mm.; length of wing (estimated) about 5.25 mm.

MALE

HEAD (FIG. 78A): Reddish yellow, including usually the entire scape and the first joint of the flagellum. The subsequent joints of the flagellum sometimes coal black throughout, sometimes more or less ferruginous below, particularly towards the base. The area of black beneath the ocelli more extensive than in the worker, subtriangular with the down-pointing angle extending usually to the supraclypeus. The labrum blackish and the mandibles black except for their red apical one-third. The inner orbits of the eye flanked usually by a more vivid yellowish than the contiguous part of the head, almost giving the effect of a band. The hairs on the vertex and those fringing the mandibles below with some dark admixture but not so uniformly blackish as the hairs in the corresponding regions of the worker, in most specimens predominantly grayish.

THORAX: Except for the red scutellum and sometimes red axillae, black. The hairs more or less dark on mesonotum, mesopleura, and scutellum. The propodeum dark.

LEGS: Black, with more or less invasion of brownish, the anterior pair often lighter on the under side of trochanters, outer face of tibiae, and the tarsal joints. The hairs mostly black, but those on the under side of the trochanters and femora, particularly of the fore and middle legs, tend to be pale, and the microscopic hairs that rather densely cover the posterior slope of the under side of the hind tibiae are silvery gray. (Fig. 78B.)

WINGS: With the same somewhat darkened areas noted for the worker and with the color of the neuration as set down for that caste, but sometimes, judging from Smith's description, with wings presenting the alternate condition noted in the case of the worker. Number of hamuli per lower wing ranges from six to seven. Of 30 wings examined, 15 had six hamuli and 15 had seven hamuli, an average of 6.5.

ABDOMEN: Reddish, usually somewhat

clouded, especially dorsally. The bristles towards the apex of the abdomen in dorsal aspect black. Some black bristles flanking sternites 4 and 5 but the sericeous hairs on these and the previous sternites silvery gray.

MEASUREMENTS: Length 4.75 to 5.75 mm.; width of thorax about 1.75 mm.; length of forewing, including tegula, about 5.25 mm.

TYPE MATERIAL

Described from Brazil. See comments under discussion.

DISCUSSION

Smith's description of *tataira* (1863a, p. 508) is difficult to interpret. In all likelihood his material was either composite or, what seems still more probable, it included callows as well as fully colored individuals. He speaks of the thorax as black, which is the condition in what H. Müller (1874, p. 31) described subsequently as *cagafogo*, but adds, "sometimes with an obscure testaceous broad stripe running down the center of the mesothorax and uniting with the pale colouring of the scutellum," which is true of some Brazilian specimens but is even more typical of *mediorufa* from Central America, the insect that Cockerell (1917, p. 124) made the type species of his subgenus *Oxytrigona*. Smith's reference to the coloration of the wings in his description of *tataira*, "the wings hyaline, their nervures rufo-testaceous," also seems more applicable to *mediorufa* than it does to *cagafogo*, which, according to Müller's description, has the basal portion and the radial cell of the forewings dark fuscous. Yet *cagafogo* is usually made a synonym of *tataira*.

Frederick Smith's description of *tataira* was based on the male. The specimen designated as the type in the British Museum (Natural History) is, however, a worker. This worker bears, in addition to the type ticket, a label that reads: "Smith coll. Pres. by Mrs. Farren White 99-303." It is a specimen that represents the condition especially characteristic of *mediorufa* in having a median area of red down the otherwise black mesonotum. This, too, is the condition of a male specimen at Oxford University identified by Smith as *tataira*, and also of a male specimen in the American Museum similarly identified by Smith. These males have the

upper half of the mesopleura and the middle and hind legs above the tibiae tawny; workers, on the other hand, of both *cagafogo* and of *mediorufa* have the corresponding areas black, and this is true also of the male of *cagafogo*. The male at Oxford University and the male at the American Museum are different in coloration from the males accompanying workers from Massaranduba-Blumenau that are indubitably the same as Müller's *cagafogo*. These two males have indeed certain resemblances to yet another form, *flaveola* Friese.

It is with diffidence, therefore, and somewhat arbitrarily that I am interpreting Smith's *tataira* as the earlier name for *cagafogo*. My justification for doing so is that the form of more completely dark thorax seems to constitute the standard part of Smith's description, the form of variegated thorax the exception. The validity of Müller's *cagafogo* as a form independent of typical *tataira* would seem to derive some support from the claim of Müller that "Mr. Frederick Smith has been good enough to compare my [H. Müller's] specimens with the collection in the British Museum and has found that they belong to an undescribed species." However, it is not impossible that Smith's examination was superficial, for among the specimens lent me by the British Museum (Natural History) is one labeled "Smith coll. Pres. by Mrs. Farren White 99-303," and this specimen is in complete accord both as to coloration of chitin and of wings with Müller's description of *cagafogo* and with specimens from Massaranduba-Blumenau.

Occasional workers (probably callows) occur that, although in accord with the typical form in respect to the darker coloration of their wings and the presence of black hairs on the sternites of the abdomen, nevertheless are like *mediorufa* in respect to the coloration of the thorax, but now and then a specimen is found that even shares the wing coloration of *mediorufa* and shows its affiliation with typical *tataira* only in the color of its hairs. Typical *tataira* is a form of southern range, more particularly Brazil, and *mediorufa* is found in Central America. Owing to lack of standardization in the coloration of the thorax and even of the wings, the most trustworthy character for separating typical

tataira and *mediorufa* would seem to be the coloration of the hairs.

The description of the queen is based on a single individual from Massaranduba-Blumenau, Brazil, and the coloration noted may not be constant. The maculation of the mesonotum observed in the case of this individual marks a transition to that of the worker of *mediorufa* but resembles even more closely (but in reverse coloration) the queen of *Trigona* (*Cephalotrigona*) *capitata* variety *zexmeniae* Cockerell, the basic coloration of the mesonotum in the queen of *zexmeniae* being red and the separating stripes black, whereas in the queen of *tataira* it is the separating stripes that are red and the basic coloration that is black (pp. 455, 472).

The species *tataira* belongs to a subgenus that is particularly dreaded because its attacks so often result in painful after-effects to the individual victimized. An account of the nature of the attack and the results produced is given in the discussion of the subgenus. In view of the effectiveness with which *tataira* ordinarily wards off human intruders, it comes as somewhat of a surprise that this species sometimes itself falls victim to the attacks of other species of stingless bees. At least that is the interpretation that must be placed on H. von Ihering's observation (1903, pp. 260-261) that "*dorsalis*"¹ is an enemy of this species as well as of other bees. "After years of painstaking effort," wrote von Ihering, "I succeeded in locating a nest of *Trigona cagafogo*, feared on account of its painful bite, but when at last the nest was to be called for, it had been destroyed by a swarm of *Trigona dorsalis* which had made its nest in the hive. The seizure of the nest is achieved after intense combat, in which the bees offering resistance are killed. In these struggles *Trigona dorsalis* comes out the victor if for no other reason than that its somewhat more powerful mandibles assure it a certain superiority over its opponents. Only the dwelling is utilized by the robbers; the brood-combs and the provision-containers are destroyed and removed, being replaced respectively by others newly constructed."

¹ I think it doubtful whether von Ihering's "*dorsalis*" is the same as that described by F. Smith (1854, p. 411). More likely it is a form close to *postica*.

In connection with the attacks of "*dorsalis*" on *tataira* as recorded by H. von Ihering, it is of interest to note that Girard (1875a, p. 572) mentioned "*dorsalis*"¹ as a probable combatant of *flaveola*, here considered merely a variety of *tataira*.

According to H. Müller (1875b, p. 48), the floral visits of *tataira* are few and confined largely to ill-smelling plants. In an earlier paper (1874, p. 32) he cited the observations of his brother, F. Müller, who had noted *tataira* "visiting in swarms the flowers of a bean with glandular calyx; also a white-flowered *Abutilon* and *Sicyos angulata*, the flowers of which are glandular and secrete an oil. It was also observed fertilizing the flowers of *Asclepias curassavica* . . . repeatedly sucking the juice flowing out of trees, and devouring the sugar spread to be dried." Ducke (1907, p. 89) collected *tataira* on the flowers of *Byrsonima*, and Bertoni (1911, p. 144) stated that in Puerto Bertoni, Paraguay, one of the flowers most frequently visited by *tataira* was the banana (*Musa*).

If floral visits be selective, other sources of liquid supply are not neglected. F. Müller was the first to note that *tataira* has the interesting habit, shared with some of the ants, of exploiting membracids for their secretions. The observation has been confirmed in the case of another *Oxytrigona* (see discussion of *mediorufa*) and is quite possibly general throughout the subgenus. As stated by H. Müller (1873, p. 201), his brother (F. Müller) "found the pedunculi of the flowers of *Cassia multijuga* pretty frequently occupied by societies of larvae of this species [subsequently identified as probably *Potnia indicator* (H. Müller, 1874, p. 31)] closely crowded together. Amongst these larvae there was present a great number of the above-mentioned *Trigona*, marching all the day long amongst and upon them. When taken between the fingers, the larvae of the Membracids immediately emitted a little drop of a limpid fluid from the upward bent tip of their abdomen—probably a sweet fluid, for the sucking of which the larvae are visited by the *Trigona*."

Other fluids, too, but of a more revolting

character are also lapped up by *tataira*. According to H. Müller (1873, p. 201), his brother once found a multitude of *tataira* "spread over the body, already strongly putrefying, of a large toad; the interior of the large open mouth of the toad, was filled with these bees, probably sucking the putrid juice of the dead body. On another occasion he saw a great number of the same species of bees in the putrefying intestines of a hen." Also a bee of this species alighted on F. Müller's hand as he was cleaning the skull of a poisonous snake (H. Müller, 1875b, p. 48). The bee is "fond of old stinking cheese" (H. Müller, 1874, p. 32). H. von Ihering (1903, p. 206) likewise bore testimony to the fact that *tataira* is frequently found on carrion.

Influenced no doubt by memories of the carrion-visiting habits of *tataira*, F. Müller found its honey somewhat disagreeable as well as insipid. Others, perhaps unaware of these unpleasant visitations, have considered the product palatable. Smith (1863a, p. 499) characterized the honey of *tataira* as "excellent," but it is possible that his praise of its quality was based not on a personal sampling of the honey but on the report of Gardner (1846, p. 327; 1849, p. 249), who used this very adjective in describing the honey of *tataira*. Gardner's *tataira*, it is true, was very possibly not typical *tataira*, for Gardner refers to the bee as having a yellow body and a black head, which is inaccurate. Peckolt (1894, p. 223), who described *tataira* in the same terms as Gardner, pronounced the honey as pleasant to the taste. Spix and Martius (1828, p. 542), indicated that the honey of "Caca-Fogo," believed to be the same bee as *tataira*, was not unappreciated by the Brazilians, who went to the trouble of gathering the honey by night in order not to subject themselves to the painful attacks inevitable during a daytime foray on the nest.

The aggressiveness of bees of the subgenus *Oxytrigona* and the peculiar injury they inflict are discussed in the section devoted to this subgenus (p. 468). Several of the instances there enumerated are attributable to typical *tataira*. Animals as well as man are attacked by these ferocious bees. Marianno even recounted (1911, p. 85) an assault which was made on a colony of the honeybee, *Apis mellifera*. The legitimate occupants of the

¹ Likewise presumably a bee close to *postica* rather than true *dorsalis* F. Smith.

hive put up no defense against the aggressors, who invaded the hive, robbing it in a few days of all its existing provisions. R. von Ihering (1940, p. 188) likewise alluded to attacks by *tataira* on *Apis mellifera*.

So far as reported, the nests of *tataira* are all located in the hollows of trees. The earliest mention made to that effect is perhaps that of Coelho de Scabra (1799, p. 103). F. Müller noted two nests that were thus ensconced, one of them 5 meters above the ground (H. Müller, 1874, p. 32). Gardner (1846, p. 327; 1849, p. 249) mentioned *tataira* as one of 11 species that constructed their nests in the hollow trunks of trees, and a nest reported by H. von Ihering (1903, p. 206) was likewise thus sheltered. Peckolt (1894, p. 223) mentioned nests in tree hollows and that is also the nesting site mentioned by Ambrosetti (1895, p. 699). In confirming the fact that *tataira* "nests always in trees" Marianno (1911, p. 85) added the further impression that it "prefers humid places, little exposed to the sun." Bertoni (1911, p. 144) supplied further instances to the mounting testimony that it is hollow trees these bees select as nest sites. In view of the unanimity of these observations it seems reasonably certain that *tataira* and, so far as reported, also the other representatives of the subgenus *Oxytrigona* are not nearly so adaptable in the selection of a nest site as are many of the species of other subgenera. Yet occasionally even *Oxytrigona* will assert its independence and depart from the standard pattern (see the discussion of the variety *flaveola*).

Rodolpho von Ihering (1940, pp. 187-188) explained the fact that the entrance to the nest of *tataira* is through a crevice in the bark of the tree by saying that such a portal suffices for an aggressive species whereas timid species make large portals with various small entrances. But one need cite only the conspicuously large entrance tube of a belligerent species like *Lestrimelitta limão* (F. Smith) to indicate that this distinction has its exceptions.

According to R. von Ihering (1940, p. 133), "barra-fogo" as well as "caga-fogo" is a common name applied to *tataira*.

DISTRIBUTION

Ducke, whose description of *tataira* (1925, p. 369) included, like that of Smith, indi-

viduals of somewhat divergent character, listed several Brazilian states in the range, namely, Maranhão, Ceará, Minas Gerais, Rio de Janeiro, São Paulo, and Santa Catharina. Ducke also included Paraguay, on the authority of Strand (1910, p. 559) and Bertoni (1911, p. 144) and Bolivia within the range of *tataira*. Raveret-Wattel (1875, p. 738) indicated that "tataira" is found in the States of Parahyba and Pernambuco.

Among the specimens before me those that conform with typical *tataira* as here interpreted are from the following localities:

BRAZIL: State of Bahia: Bahia, March 13, 1883. State of São Paulo: São Paulo, 1897 (von Ihering); Bauru. State of Santa Catharina: Blumenau, Oct., 1898 (Virgil); Massaranduba-Blumenau, Sept.-Oct. 1935, including queen and males (K. Schmith). State of Minas Gerais: Barro Alto, Nov., 1931 (José Blaser).

BOLIVIA: Rio Colorado, Sept. (W. M. Mann).

Trigona (Oxytrigona) tataira variety *mediorufa* Cockerell

Trigona flaveola mediorufa COCKERELL, 1913a, pp. 12-13.

Trigona flaveola mediorufa, WHEELER, 1913, pp. 8-9.

Trigona (Oxytrigona) salvatoris COCKERELL, 1917, pp. 124-125.

Trigona (Oxytrigona) tataira mediorufa, COCKERELL, 1917, p. 125.

Trigona flaveola mediorufa, LUTZ AND COCKERELL, 1920, p. 497.

Trigona flaveola, WHEELER, 1923, p. 122.

Trigona salvatoris, LUTZ, 1924a, pp. 205, 207, 208, 216, 220 (identified by T. D. A. Cockerell).

Trigona (Oxytrigona) mediorufa, SCHWARZ, 1932a, p. 248.

Trigona flaveola variety *mediorufa*, MAIDL, 1934, p. 316.

WORKER

DIAGNOSTIC CHARACTERS: Head predominantly reddish yellow to orange ferruginous. Mesonotum with the median one-third red, the flanking thirds black. Scutellum and usually axillae orange ferruginous. Mesopleura predominantly black. Middle and hind legs, at least, predominantly dark. Wings hyaline to slightly milky, with median cell sometimes faintly orange tinted. Abdomen orange ferruginous. Hairs of body range for most part from pale to fulvous; dark hairs on tibiae, outer face of metatarsi, and apical tergites of abdomen.

HEAD: Reddish yellow to orange ferruginous, with the following exceptions: the scape blackened posteriorly towards the apex; the flagellum darkened above and also (except for the apical margins of the joints) below; the region between and particularly below the ocelli black, the black variable in amount, usually with lateral processes; a transverse dark subapical line usually on the clypeus; in addition the clypeus is apt to be very narrowly outlined in black along its base and sides; the apical edge narrowly, and the basal prominences on the mandibles, more or less darkened. The hairs on the vertex fulvous, those on the labrum and fringing the mandibles below pale to ferruginous.

THORAX: The pronotum largely or wholly orange ferruginous, including the tubercles. The mesonotum with the middle one-third orange ferruginous, the lateral thirds black but bordered outwardly by a stripe of orange ferruginous. The axillae usually and the scutellum orange ferruginous, the scutellum narrowly blackened along its base. The mesopleura, metapleura, and propodeum black. The hairs of the mesonotum "red on the red parts but mainly fuscous on the black" (Cockerell, 1913a, p. 12) but more often pale red throughout (in some lights almost silvery gray) as are the hairs of the mesopleura and those on each side of the shiny central area of the propodeum.

LEGS: Black to reddish black in the case of the middle and hind pair except for the sometimes paler middle trochanters, spot sometimes at apex of middle femora and base of middle tibiae, and the usually somewhat paler small joints of tarsi. The fore pair of legs of lighter hue than the middle and posterior pair, with the trochanters, anterior face of femora, tibiae anteriorly and often externally, and the small joints of the tarsi reddish, but even the other parts of these legs as a rule only lightly clouded. The hairs on the coxae, trochanters, and for the most part on the femora of all of the legs pale; those on the tibiae and the external face of the metatarsal joints black, but the microscopic hairs on the raised surface of the inner face of the hind tibiae are silvery gray and the metatarsal brushes more or less reddish golden.

WINGS: Hyaline to more or less milky,

with the median cell sometimes faintly orange tinted; stigma and veins light orange ferruginous. Tegulae approximately concolorous with the venation. Number of hamuli per lower wing usually six, rarely seven, and still more rarely five. Of 106 wings examined, 95 had six hamuli, nine had seven hamuli, and two had five hamuli, an average of 6.06.

ABDOMEN: Orange ferruginous. The hairs on tergites 3 to 5 more or less blackish or brownish viewed from the side but rather fulvous viewed from above; the hairs on tergite 6 sometimes dark, sometimes fulvous. The hairs on the sternites distinctly fulvous and without dark admixture.

MEASUREMENTS: Length 4.5 to 5.5 mm.; width of thorax about 1.75 mm.; length of forewing, including tegula, about 5.25 mm.

QUEEN

Unknown.

MALE

Unknown.

TYPE MATERIAL

Trigona (Oxytrigona) tataira variety *mediorufa* Cockerell was described on the basis of three specimens from Escuintla, Guatemala. The holotype is in the American Museum of Natural History, and one of the paratypes is in the British Museum (Natural History). The type (from San Salvador, El Salvador) and the cotype (from Escuintla, Guatemala) of *salvatoris*, hardly separable from *mediorufa*, are in the United States National Museum.

DISCUSSION

The character principally to be relied upon in separating workers, at least, of *mediorufa* from typical *tataira* is the color of the hairs of the head, thorax, and abdomen, which tends to be fulvous in *mediorufa* and black in *tataira*. The contrast is especially strong in the case of the hairs of the abdominal sternites. The character that gives *mediorufa* its name (the reddish color of the median one-third of the mesonotum) is shared by occasional specimens (probably callows) of typical *tataira*, although as a rule this area is, as is the rest of the mesonotum, black in typical *tataira*. The usually dark staining of the basal half of the wing and of the marginal cell in

typical *tataira*, and its rather dark nervures, are other characters that usually can be relied upon to separate *tataira* from *mediorufa*, which has honey-colored neurulation.

Cockerell erected as a separate species, or as a separate subspecies of *tataira*, or finally as a race of *mediorufa*, what he described (1917, p. 124) as *salvatoris*. His hesitation may indicate the difficulty in arriving at an appraisal of the relationship of closely allied forms within the *tataira* group, and the *tataira* group is merely typical of the comparable problems presented by other interdigitated and overlapping forms within *Trigona*. The characters that Cockerell gave for separating *salvatoris* are as follows: "Closely allied to *T. mediorufa* (Cockerell), with the same black and red pattern of mesothorax, but differing thus: head black (faintly reddish), the clypeus dull yellow with two dark marks, a pale spot behind lower end of eye (in immature specimens the whole head dusky reddish); scape dark reddish; posterior half of abdomen suffusedly dusky."

I find it hard to draw a sharp distinction between the two alleged forms, which seem to me to intergrade between a cloudy and a clear condition of red in the case of the head. In extreme cases the scape, too, is largely black instead of black only posteriorly at the apex (the usual condition in *mediorufa*) but again with intergrading specimens tending to link the extreme with the usual. Cockerell's type and cotype of *salvatoris* indeed offer evidence of gradation in themselves. The type has the head much darker than in the cotype. The longitudinal marks on the clypeus are very faint in the cotype, a transition apparently to the spotless condition of the clypeus usual in typical *mediorufa*. The type material of *mediorufa* and part of the type material of *salvatoris* came from the same locality (Escuintla, Guatemala), and it is the Escuintla specimens in particular that are open to suspicion. I am inclined to regard them as virtually the same as *mediorufa*. Certainly their relationship to that form seems closer than the relationship between typical *tataira* and some of the aberrant specimens linked with it. A slight obscuration of the yellow of the face in some of the specimens here assigned to variety *obscura* would necessitate a recognition of these specimens

as an independent variety if the same standard were applied that Cockerell brings to bear in the case of *mediorufa* and *salvatoris*.

Some 70 years ago F. Müller observed typical *tataira* in southern Brazil in attendance on membracid nymphs, sucking the fluid that these nymphs emitted (H. Müller, 1873, p. 201; 1874, p. 31). A similar observation on *tataira* variety *mediorufa* in Guatemala was communicated to me by M. Bates.

As are other members of the subgenus *Oxytrigona*, the variety *mediorufa* is among the most aggressive and obnoxiously equipped of all the stingless bees. The reader is referred to the discussion of the subgenus (p. 469) for an account by Wheeler (1913, p. 8) of the nature of its attack and the character of the injuries it inflicts.

The colony that attacked Wheeler had its nest "about four feet from the ground in the trunk of a large tree. There was no cerumen spout to the nest entrance, which was a hole about 3/4 inch in diameter, guarded by a company of workers, all with their shining yellow faces directed toward the outside."

One is tempted to believe that it is *mediorufa* to which Bell (1899, p. 233) refers in his account of stingless bees occurring on the Mosquito Coast of the Caribbean Sea (between latitudes 11°00' and 15°00' N.). Bell mentions "patera" as the popular name of a bee that "defends its nest stoutly, pursues the aggressor, alights on the skin, and deposits a minute drop of milky fluid which soon begins to smart, and after a while festers, and may turn into a troublesome sore." The account at least tallies in the main with what we know of *Oxytrigona*.

This bee, like other members of the subgenus *Oxytrigona*, has an unpleasant odor, due to its secretion. Wheeler (1913, p. 8) compared the odor to that of rancid butter, which is the very term he applied also to the odor given forth by a colony of *Trigona* (*Trigona amalihea* (Olivier) that was on the point of swarming. It is a smell characteristic, too, of ants of the genus *Tapinoma*.

DISTRIBUTION

Described from Guatemala and represented in the collections before me from the following localities in that state:

GUATEMALA: Escuintla, Aug. 9 (F. Knab), and

Dec. 30, 1911 (W. M. Wheeler); Chiquimulilla, 300 meters, Department of Santa Rosa, March 21, 1923, and April 1923 (René Lichy); Santa Emilia, Pochuta, 1000 meters, Feb.-March, 1931 (J. Bequaert); Moca, Guatallon, 1000 meters, March-April, 1931 (J. Bequaert).

Variably darker and hence more or less approximating Cockerell's conception of *salvatoris* are specimens from the following localities:

EL SALVADOR: San Salvador, Aug. 15 (F. Knab).

GUATEMALA: Finca Buena Vista, San Sebastian, Feb. 18, 1930, attending membracids (M. Bates).

MEXICO: State of Chiapas: Tapachula, "in dense group on a tree trunk 60 cm. above ground" (A. Dampf).

Trigona (Oxytrigona) tataira variety
flaveola Friese

Trigona flaveola SPINOLA, 1840, p. 124. (Named by Illiger without description.)

? *Trigona flaveola*, ERICHSON, 1841, p. 219.

"Caga fogo," DRORY, 1873a, pp. xxxi, xxxii.

Trigona flaveola, DRORY, 1874, pp. 281, 282, 284, 285.

Trigona flaveola, GIRARD, 1875a, pp. 572, 573.

Trigona flaveola, RAVERET-WATTEL, 1875, pp. 738, 739, 741, 743.

Trigona flaveola, GIRARD, 1876a, pp. 193, 194.

Trigona flageola (*sic*), DRORY, 1877, pp. 147-148.

Trigona flaveola, TASCHENBERG, 1877, pp. 216, 218.

Trigona flaveola, GIRARD, 1879, pp. 708, 711-712, 716.

Trigona flaveola, TOMASCHEK, 1880, p. 63.

Trigona flaveola, TASCHENBERG, 1892, pp. 230, 232.

? *Melipona caga-fogo*, PECKOLT, 1894, p. 225.

Trigona flaveola FRIESE, 1900a, p. 389.

Trigona flaveola, SILVESTRI, 1902b, pp. 144-145.

Trigona flaveola, BUTTEL-REEPEN, 1903a, p. 145.

Trigona flaveola, HAMLYN-HARRIS, 1903, p. 100.

Trigona tataira variety *flaveola*, DUCKE, 1916, opposite p. 28, pp. 42-43.

Trigona (Oxytrigona) tataira friesiella COCKERELL, 1917, p. 124.

Trigona tataira friesiella, LUTZ AND COCKERELL, 1920, p. 501.

Trigona flaveola, PHISALIX, 1922, p. 429.

Trigona flaveola, LUTZ, 1924a, pp. 205, 207, 214, 220 (identified by H. Friese).

Melipona tataira variety *flaveola*, DUCKE, 1925, pp. 342, 369-370.

Trigona flaveola, MAIDL, 1934, p. 316.

Melipona tataira variety *flaveola*, DUCKE, 1945, opposite p. 24, pp. 35-37.

WORKER

DIAGNOSTIC CHARACTERS: Head predominantly reddish yellow to orange ferruginous, as is the thorax. The latter usually with a dark cuneiform maculation at each side of the mesonotum and usually also with a dark spot on lower half of mesopleura. Legs with basal joints to inclusion of femora predominantly fulvous, and some or all of the joints below the femora predominantly black. Wings as in *mediorufa*. Hairs of body range from pale to fulvous but black on tibiae, external face of metatarsi, and apical tergites of abdomen.

HEAD: Reddish yellow to orange ferruginous with the following exceptions: the flagellum above except for the basal two joints, which may be wholly fulvous, and the scape sometimes blackened posteriorly on more or less of its apical half (specimens from Río Colorado, Bolivia, and Chapada, Brazil); the flagellum below frequently wholly fulvous but in the other cases (specimen from Río Colorado, Bolivia) only the apical margins of the joints are fulvous, the basal part darkened; the apical edge of the mandibles narrowly darkened and their basal prominences touched with black; the clypeus faintly and narrowly outlined in reddish to blackish, a narrow transverse dark stripe sometimes present along its apical border and more rarely (specimens from Chapada, Brazil) a short longitudinal dark mark at each side of its middle. The ocelli sometimes narrowly but as a rule discontinuously rimmed with black, no extensive spread of black in the ocellar region. The hairs of the head fulvous.

THORAX: Almost wholly reddish yellow to orange ferruginous. Usually, however, with a more or less well-developed, cuneiform, dark maculation at each side of the mesonotum (a few of the specimens from Tumupasa and Ivon, Río Beni, Bolivia; nearly all of the specimens from Río Colorado, Bolivia, and from Chapada, Brazil; and all of the specimens from Tarata and Mapiri, Bolivia) and usually a black maculation, especially anteriorly, on the lower half of the mesopleura (reduced to absent in specimens from Ivon,

Río Beni, and Tumupasa, Bolivia). The bare median area of the propodeum concolorous with the thorax or barely darkened. The hairs fulvous, especially on the mesonotum and scutellum, tending to become a little paler towards the lower part of the mesopleura. The erect hairs among the silvery gray tomentum at each side of the propodeum more or less silvery gray to fulvous in some lights.

LEGS: Variable in coloration but at least the coxae, trochanters, and femora predominantly fulvous, and some or all of the joints below the femora predominantly black. Usually there is a more or less developed black stripe on the under side of all the femora (absent in the case of the fore femora, however, in specimens from Mapiri, Tarata, and Ivon, Río Beni, Bolivia, and from Chapada, Brazil), and sometimes the upper part of the femora is streaked or cloudy. The fore tibiae sometimes wholly or almost wholly fulvous (specimens from Mapiri, Tarata, and Ivon, Río Beni, Bolivia, and some of those from Chapada, Brazil), sometimes extensively clouded or mottled with black on their external face (specimens from Tumupasa, Bolivia) and sometimes black externally except for a basal spot (specimens from Río Colorado, Bolivia). The middle tibiae fulvous, slightly mottled with black externally (specimens from Ivon, Río Beni, Bolivia) or, more often, largely black or dark brown externally except for a basal and sometimes also an apical spot of fulvous (specimens from the other localities). The hind tibiae black or dark brown externally except for an emargination anteriorly shaped much like the hind tibia itself (specimens from Ivon, Río Beni, Bolivia) or more extensively to wholly black or dark brown with sometimes a narrow lighter area anteriorly and often, as well, a pale maculation at the base (specimens from the other localities). The inner face of the hind tibiae also variable, sometimes fulvous, sometimes fulvous rimmed posteriorly with black, sometimes with only the median area fulvous or with even that obscured. All the metatarsi externally and usually the subsequent tarsal joints, with the exception of the apical one, black; in specimens from Ivon, Río Beni, Bolivia, the dark maculation on the fore

metatarsi is often very feeble. The hairs on the coxae, trochanters, and for the most part of the femora of all of the legs pale; those on the tibiae and the external face of the metatarsal joints black, but the microscopic hairs on the raised surface of the inner face of the hind tibiae are silvery gray and the metatarsal brushes more or less copper hued.

WINGS: Hyaline to slightly milky, with the median cell faintly orange stained; stigma and veins light orange ferruginous. Tegulae approximately concolorous with the venation. Number of hamuli per lower wing usually six or seven, rarely eight. Of 107 wings examined, 45 had six hamuli, 59 had seven hamuli, and three had eight hamuli, an average of 6.61.

ABDOMEN: Usually orange ferruginous but sometimes more or less clouded, especially dorsally, to even fulvous (specimens from Chapada, Brazil). The hairs on tergites 3 to 6 black in contrast to the pale to fulvous hairs on the sternites.

MEASUREMENTS: Length 4.25 to 6.25 mm.; width of thorax about 1.75 to 2 mm.; length of forewing, including tegula, about 5.25 to 5.5 mm. (the specimens of slightly longer wing are from Tumupasa, Río Colorado, Mapiri, and Tarata, Bolivia).

QUEEN

Unknown.

MALE

Unknown.

TYPE MATERIAL

The type material of *flaveola* included specimens from Colombia, Guatemala, and Brazil. Friese does not indicate the depositary of this type material. Metatypes from Tarata and Mapiri, Bolivia, are in the American Museum of Natural History.

DISCUSSION

It seems probable that what Friese (1900a, p. 389) described as *flaveola*, renamed *friesiella* by Cockerell¹ (1917, p. 124), was com-

¹ I do not see justification for abandoning Friese's name. Cockerell rejects the designation of *flaveola* "as there is an earlier *T. flaveola* Spinola." The only reference to *flaveola* that I have succeeded in tracing in the published work of Spinola is that which occurs in Spinola's paper of 1840. In that paper selection of the

posite, for it was based on specimens from both South and Central America. According to Cockerell (1913a, p. 12) Friese regarded Cockerell's *mediorufa* as synonymous with his own *flaveola*, and it is possible that Friese's Guatemalan specimens were of the same character as *mediorufa*, which was also described from Guatemala, or even *mellicolor* (see distribution of that variety). But, as Cockerell pointed out (1913a, p. 12), there are elements in Friese's description of *flaveola* which do not apply to *mediorufa* but which do apply to metatypes before me of *flaveola*, and I am in accord with Cockerell that recognition should be given to *mediorufa* as a form distinct from those specimens to which Friese's description of *flaveola* applies.

The specimens assigned to *flaveola* in this paper show considerable diversity as the redescription I have given makes clear. Such a character as the presence or absence of two dark cuneiform maculations of the mesonotum might seem to afford a line of distinction, but it cannot be applied absolutely even among the specimens of a single locality. The maculation of the legs also shows considerable variability, although as a general rule the joints above the tibiae tend to be predominantly fulvous, those from the tibiae downward predominantly black. Particularly is this true of the middle and hind legs.

name *flaveola* is attributed by Spinola (p. 124) to Illiger. But the name is unaccompanied by a description, and in the published papers of Illiger I also fail to find a description of *flaveola*. It would seem to have the status merely of a manuscript name.

Curiously enough, there is mention of a *flaveola* also by Girard—first in 1875a (pp. 572 and 573) and later in 1876a (p. 194). In the later paper the name *flaveola* is used in association with the popular name of the bee, namely, "caga-fogo," which places Girard's *flaveola* rather definitely in the *tataira* group. Finally in 1879 (pp. 711-712) Girard again applies the term *flaveola* and "caga-fogo" to the same bee. If the bee that Girard interpreted as *flaveola* is the same that Illiger and Spinola so designated, then all of these must have been close, at least, to the bee that Friese subsequently described as *flaveola*. The same conclusion applies also beyond a doubt to the *flaveola* (misspelled *flageola*) that Drory (1877, pp. 147-148) commented upon, for Drory gave as its popular name "caga fogo" and proceeded to recount the devastating character of its attack, so closely in accord with what we know to be true of Friese's *flaveola*, and the persistence of the burns which it produces. In Drory's case the vestiges of these were still in evidence after two months or more.

The specimens from Chapada (Brazil) duplicate within *flaveola* much the same tendency to independence that is shown by *salvatoris* within *mediorufa*. In the Chapada specimens, as in *salvatoris*, the head tends to be darker, there are often two short dark stripes on the clypeus, and a yellow stripe near the lower end to the outer orbit of the eye. The abdomen in these specimens is frequently darkened.

It is possible that the bee that Peckolt (1894, p. 225) referred to as "caga-fogo" is the variety *flaveola*. Peckolt described it as having a red head, yellowish red thorax, and yellow shiny abdomen—characters that among the South American *Oxytrigona* apply best to *flaveola*. He came upon its nest in the primeval forest. It was located on a tree, about 3 meters from the ground, "in a voluminous heap of aerial roots of an epiphytic pineapple-growth."

DISTRIBUTION

This variety was described from Colombia, Guatemala, and Brazil, but the Guatemalan specimens, at least, may have been variety *mediorufa* or *mellicolor*. The specimens before me are mostly from Bolivia, with a few from Brazil, as follows:

BOLIVIA: Tarata, 1900; Mapiri, 1900; Ivon, Río Beni, Feb. (W. M. Mann); Río Colorado, Sept. (W. M. Mann and Lopez); Tumupasa, Dec. (W. M. Mann).

BRAZIL: State of Matto Grosso: Chapada (probably Sant' Anna do Chapada, near Cuyabá) Jan.-March, May (H. H. Smith).

Trigona (Oxytrigona) tataira variety
mulfordi, new variety

WORKER

DIAGNOSTIC CHARACTERS: Head, thorax, legs, and abdomen almost wholly reddish yellow to orange ferruginous, with only a few, often faint traces of black, as follows: two spots on mesopleura (often evanescent), middle area of propodeum, under side of hind femora, apex and posterior contour of hind tibiae. Wings with median and marginal cell smoky as in *obscura*. Hairs for most part fulvous but dark on tibiae and tarsal joints externally and on tergites 3 to 6 of abdomen.

HEAD: Reddish yellow to orange ferrugi-

nous, with the following parts black: the scape briefly but emphatically towards the apex posteriorly, the flagellum above except for sometimes its two basal joints, the basal prominences of the mandibles, and narrowly their apical rim. The clypeus outlined very narrowly with black to dark reddish and a narrow transverse dark stripe sometimes just before the apical margin. Occasionally a dark spot in the malar space. The ocelli at most narrowly and incompletely rimmed with black; no extensive dark staining in the ocellar region. The hairs predominantly fulvous.

THORAX: The pronotum orange ferruginous, including the tubercles. The mesonotum almost wholly orange ferruginous, but its extreme basal border more or less rimmed narrowly with black, and this margin of black extended backward somewhat along the declivity of the sides. The steep sides of the axillae also somewhat blackened below, the fossa between the mesonotum and the scutellum narrowly dark. Beneath the tegulae a very limited area of cloudiness. The mesopleura predominantly orange ferruginous except for a small spot anteriorly at about their middle and a small spot posteriorly likewise at about their middle (both faint). The hairless middle area of the propodeum black. The hairs of the thorax throughout fulvous (in some lights almost silvery gray, especially those towards the under side of the thorax).

LEGS: Predominantly fulvous with restricted and for the most part feeble dark markings. The obscuration and its relative intensity are as follows: slightly darkened usually on the outer face of the front metatarsi; a dark spot or nebulous area usually on the apical half of the under side of the middle femora; the outer face of the middle metatarsi feebly darkened (or not at all) and the three following tarsal joints usually somewhat darkened; an area of rather intense black along the under side of the hind femora (usually more extensive than in the corresponding area of the middle femora); the external face of the hind tibiae with a more or less dark stripe (often brownish rather than black) along the posterior contour that at a little more than one-third of the distance from the apex broadens out abruptly to

becloud in full width this area of the joint; the under side of the hind tibiae usually darkened anteriorly; the external face of the hind metatarsi usually clouded anteriorly and the three following small joints of the tarsi darkened. The hairs of the coxae, trochanters, and femora of all the legs pale; those of the tibiae and tarsal joints externally blackish, with in some cases fulvous hairs intermixed on the middle and particularly on the fore tibiae. The metatarsal brushes more or less copper colored to golden. The microscopic hairs that densely cover the raised area of the inner face of the hind tibiae silvery gray.

WINGS: With the median and marginal cells and a narrow area immediately below approximately the apical half of the marginal cell strongly smoky; the other parts of the wing subhyaline to slightly milky. The neurulation and stigma brownish. The tegulae pale ferruginous. The number of hamuli per lower wing is usually six or seven, rarely eight. Of 24 wings examined, 14 had six hamuli, eight had seven hamuli, and two had eight hamuli, an average of 6.5.

ABDOMEN: Orange ferruginous, sometimes a little clouded, with dark hairs on tergites 3 to 6 but the hairs of the sternites fulvous.

MEASUREMENTS: Length 4.5 to 5.5 mm.; width of thorax about 1.5 mm.; length of forewing, including tegula, about 5 mm.

QUEEN

Unknown.

MALE

Unknown.

TYPE MATERIAL

The holotype of *tataira* variety *mulfordi* is in the United States National Museum. Paratypes are in the United States National Museum and the American Museum of Natural History.

DISCUSSION

In the coloration of its wings the variety *mulfordi* approximates the condition manifested by variety *obscura*, but while its wings tend to the dark extreme, its body coloration is among the brightest of all of the members of *Oxytrigona*, and in the predominance of

orange ferruginous and the subordination of black *mulfordi* comes closest to a form like *mellicolor*. Although specimens of variety *flaveola* were collected at both Ivon, Río Beni, and Tumupasa, where specimens of *mulfordi* were also obtained, there are no intergrading specimens that would link *mulfordi* with *flaveola*. Not only in their wing coloration but in their maculations, too, the specimens of one variety stand apart from the specimens of the other variety.

The locality records for variety *mulfordi* also correspond with localities where specimens of variety *obscura* were obtained, and the possibility has been weighed whether *mulfordi* may be merely a callow of *obscura*. Such a possibility is admitted. On the other hand, the rather close uniformity of appearance among the specimens of *mulfordi*, the relatively slight extent to which individuals among them depart from a common standard, and the absence of intergrading specimens that might link them with *obscura* have prompted me to give them a varietal name.

If the conclusion that they are not callows of *obscura* is valid, it is interesting to find three varieties of this rather rare subgenus occupying the same localities. Here is a case plainly where the term variety has no implication of geographic race.

DISTRIBUTION

Known as yet only from Bolivia, where specimens were collected in the course of the Mulford Biological Expedition of 1921-1922, as follows:

BOLIVIA: Tumupasa, Dec., including holotype (W. M. Mann); Ivon, Río Beni, Feb. (W. M. Mann).

Trigona (Oxytrigona) tataira variety *mellicolor* Packard

Trigona mellicolor PACKARD, 1869a, p. 56.

Trigona mellicolor, COCKERELL, 1907, p. 36.

Trigona (Oxytrigona) mellicolor, COCKERELL, 1917, p. 125.

Trigona mellicolor, COCKERELL, 1922, p. 8.

Trigona mellicolor, LUTZ, 1924a, pp. 205, 208, 216 (identified by T. D. A. Cockerell).

WORKER

DIAGNOSTIC CHARACTERS: Head, thorax, legs, and abdomen honey colored to reddish

yellow, with minimum traces of black, most conspicuous of which are frequently a spot on the mesopleura and almost always the bare middle region of the propodeum. Wings hyaline to very slightly milky, with median cell sometimes orange tinted. Hairs fulvous to ochraceous or paler.

HEAD: Honey colored to reddish yellow, the antennae sometimes concolorous with the rest of the head, but in other cases the scape is slightly darkened at its apex posteriorly and the flagellum is blackish or reddish black, especially above. The ocellar region sometimes without darkening, in other cases with a variable amount of black between and below the ocelli. The mandibles barely darkened on their basal prominences and narrowly along their apical edge. The clypeus very narrowly outlined with black along its base and sides, with a feeble transverse darkish stripe sometimes just before the apex and now and then an equally feeble pair of short longitudinal stripes on its middle (like those noted by Cockerell for *salvatoris*). The hairs of the head fulvous to ochraceous.

THORAX: Honey colored to reddish yellow, sometimes without any darkened areas whatever and with even the propodeum concolorous with the thorax, but usually the lower half of the mesopleura bears a dark maculation that is sometimes entire and sometimes fragmented. There is, in addition, frequently a narrow edging of black about the mesonotum, a small dark spot sometimes below the tegulae, and almost invariably the bare middle area of the propodeum is blackened. The hairs fulvous to ochraceous, especially on the mesonotum and scutellum, tending to become somewhat paler towards the lower part of the mesopleura. The erect hairs among the silvery gray tomentum at each side of the propodeum also more or less silvery gray to ochraceous.

LEGS: Exclusively honey colored to here and there reddish yellow, the deepening into reddish yellow occurring sometimes on the under side of the hind femora and often on the outer face of the hind tibiae except for a bright yellow area, in shape much like the tibia itself, that usually emarginates the reddish area anteriorly. The hairs, like those of the head and thorax, range for the most part from fulvous to ochraceous, but at least

the microscopic hairs on the raised area of the inner face of the hind tibiae silvery gray, and the metatarsal brushes, especially those of the hind pair, a little more reddish golden.

WINGS: Hyaline to very slightly milky, with the median cell sometimes faintly orange tinted; stigma, venation, and tegulae concolorous with the rest of the body. Number of hamuli per lower wing usually six, more rarely seven or five, very rarely eight. Of 182 wings examined, 128 had six hamuli, 32 had seven hamuli, 20 had five hamuli, and only two had eight hamuli, an average of 6.09.

ABDOMEN: Reddish yellow to honey colored, in exceptional cases with darkening of three or four of the apical segments dorsally and ventrally. The hairs on tergites 3 to 6 as well as the hairs on the sternites fulvous to ochraceous.

MEASUREMENTS: Length 4 to 6.5 mm.; width of thorax about 1.75 mm.; length of forewing, including tegula, about 5.25 mm.

QUEEN

Unknown.

MALE

HEAD: Yellowish to honey colored, including usually the entire scape and the first two joints of the flagellum; the subsequent joints of the flagellum black or blackish above but usually more or less furruginous below. An area of black between and below the ocelli of variable extent, in some instances reaching to or nearly to the supra-clypeus. The clypeus very narrowly outlined in black along its base and sides. The mandibles faintly and very narrowly darkened along their apical edge and usually equally faintly and restrictedly touched with black at their base. The inner orbit of the eye flanked often by a more vivid yellow than the contiguous part of the head, almost giving the effect of a band. The clypeus and supra-clypeus also usually of a stronger yellow. The hairs fulvous to ochraceous.

THORAX: Yellowish red to honey colored, sometimes without but usually with a dark maculation on the lower half of the mesopleura, sometimes with a small dark spot below the tegulae, and as a rule with an inconspicuous narrow and often fragmented dark border about the mesonotum that is

traceable usually at least along the anterior border of the mesonotum and in the fossa just before the scutellum. The bare median region of the propodeum black or blackish. The hairs fulvous to ochraceous, especially on the mesonotum and scutellum, to become slightly paler towards the lower part of the mesopleura. The erect hairs at each side of the bare area of the propodeum concolorous with the other hairs.

LEGS: Exclusively honey colored to here and there reddish, the deepening into reddish occurring sometimes on the under side of the hind femora and often on the outer face of the hind tibiae, where the area of deeper coloration occupies the posterior margin of the lower half of the joint as well as the apex of the joint. The hind metatarsi also frequently of deeper hue. The hairs, like those of the head and thorax, range from fulvous to ochraceous except for the microscopic hairs that densely cover the inner face of the hind tibiae, which are silvery gray, and the brush on the inner face of the hind metatarsi, which is sometimes rather more reddish golden.

WINGS: Hyaline to very slightly milky, with the median cell sometimes faintly orange tinted; stigma, venation, and tegulae concolorous with rest of body. Number of hamuli per lower wing usually five or six, very rarely four. Of 58 wings examined, 33 had five hamuli, 24 had six hamuli, and only one had four hamuli, an average of 5.39.¹

ABDOMEN: Reddish yellow to honey colored, usually wholly so but in exceptional cases with the apical half or more of the abdomen blackened. The hairs on the tergites as well as those on the sternites fulvous to ochraceous. The structural character of the sternites and of the genitalia is shown in figure 79.

¹ This average for the male is probably not representative. Virtually all of the specimens on which the count was based were collected at the Volcan de Chiriqui, Panama. Workers from the same locality had for the most part six hamuli per lower wing, exceptionally as few as five hamuli and very rarely as many as seven hamuli. Of a total of 36 wings of workers examined from the Volcan de Chiriqui, 31 had six hamuli, four had five hamuli, and one had seven hamuli, an average of 5.92. Although this average is higher than that for the male from the same region, it is below the average (6.09) for the worker based on specimens from a number of different localities, including the Volcan de Chiriqui.

MEASUREMENTS: Length 4.5 to 6.75 mm.; width of thorax about 1.75 mm.; length of forewing, including tegula, about 5.25 mm.

TYPE MATERIAL

The variety *mellicolor* was described from the region between Quito and the Río Napo in Ecuador. The unique type is in the Museum of Comparative Zoölogy.

DISCUSSION

The variety *mellicolor* represents the light extreme among the varieties of *tataira*, just as *obscura* stands at the dark end of the scale. The absence of black on the lower half of the mesopleura in some specimens (especially from Ecuador) and the presence of black in this region in others somewhat parallel one of the distinctions obtaining in the subgenus *Partamona* between the varieties *musarum* and *testacea*, but the specimens of *mellicolor* from Ecuador are too few to enable one to decide whether this distinction approaches constancy, and even in *musarum* and *testacea* it is not an absolute distinction.

In a letter written me from San José, Costa Rica, in 1937, F. Nevermann spoke of "a small yellow bee with amylacetate odor," the nest of which he found in a hollow cedar tree. The accompanying specimens proved to be *mellicolor*. The combs of this nest had a spiral arrangement, or at least in part a spiral arrangement, comparable with that which Nevermann had observed in nests of *Trigona* (*Trigona*) *corvina* Cockerell.

Nevermann in his letter confirms the generally disagreeable character of the members of the subgenus *Oxytrigona*. Of *mellicolor* he says: "This bee does not bite or crawl into the hair and clothes as do *corvina* and *silvestriana* but it is worse in a way for it deposits a fluid which burns slightly. The next day a heavy blister rises. The pain is enough to prevent one from sleeping if the blisters are numerous enough on arms and neck. After a week the injured area heals but a dark spot remains for about two weeks. The fluid is an acid with the scent of banana oil."

In the case of typical *tataira* it has been noted by H. Müller (1875b, p. 43) that the bee bites in the course of its attack, and in the case of the variety *mediorufa* it has been reported by Wheeler (1913, p. 8) that, in

addition to ejecting a caustic fluid, that bee, too, bites and crawls into the eyes. Nevermann's experience in escaping bites of *mellicolor* may, therefore, prove to have been exceptional rather than representative.

DISTRIBUTION

The type of variety *mellicolor* was collected in Ecuador between Quito and the Río Napo. Cockerell added another South American record when he reported (1922, p. 8) the presence of this variety in Lagunita de Aroa, Venezuela, from which I have likewise seen specimens. The form would seem, however, to be rather more abundantly represented in Central America. A specimen from Costa Rica, identified by Friese as his *flaveola*, is no other than *mellicolor* and makes one wonder whether the specimens from Guatemala that Friese (1900a, p. 389) included in his type material of *flaveola* were not really *mellicolor*. I have seen no specimens of *flaveola* from Central America, but before me are specimens of *mellicolor* from the following Central and South American localities:

HONDURAS: Tela, Guaimas District, May 1, 1923 (T. H. Hubbell); Subirana, Department of Yoro, March 7 (R. E. Stadelmann).

NICARAGUA: Chontales (Janson).

COSTA RICA: Cache (H. Rogers); Hamburg Farm, Oct. 22, 1937, including males (F. Nevermann).

PANAMA: Province of Chiriqui: Volcan de Chiriqui, 2500–4000 feet, including males (Champion); David (Champion); Progreso, April 23, 1923 (F. M. Gaige).

VENEZUELA: Lagunita de Aroa, 2000 feet (M. A. Carriker).

ECUADOR: Esmeraldas, Aug., 1908–April, 1909 (S. A. Barrett).

Trigona (*Oxytrigona*) *tataira* variety *obscura* Friese

Trigona obscura FRIESE, 1900a, p. 389.

Melipona tataira variety *obscura*, DUCKE, 1916, opposite p. 28, pp. 44–45, pl. 4, fig. 9.

Trigona tataira obscura, LUTZ, 1924a, pp. 214, 217 (identified by H. Friese).

Melipona tataira variety *obscura*, DUCKE, 1925, pp. 342, 370–371, pl. 3, fig. 6.

Trigona tataira variety *obscura*, FRIESE, 1931, p. 8, fig. 4.

Trigona (*Oxytrigona*) *tataira* variety *obscura*, SCHWARZ, 1938, p. 479.

Oxytrigona tataira obscura, MOURE, 1944a, p. 71.

Melipona tataira variety *obscura*, DUCKE, 1945, opposite p. 24, pp. 36, 37, pl. 4, fig. 9.

WORKER

DIAGNOSTIC CHARACTERS: Upper part of head black; lower half of face contrastingly pale. Thorax wholly or almost wholly black; legs and abdomen black to reddish black. Wings with the median and marginal cells and a narrow area contiguous with the apical half of the marginal cell smoky, other cells subhyaline. Hairs of body and legs predominantly black.

HEAD: Black or deep reddish black over at least the upper half of the face, vertex, and genal area (except usually for a pale area or stripe near the lower end of the posterior orbit of the eye). The mandibles also sometimes wholly black (specimens from Faro and some from British Guiana) but usually black only medianly, with a narrow basal and apical area that is deep reddish. The labrum usually more or less black or deep reddish as is as a rule the malar space. The scape usually somewhat reddish brown anteriorly, especially towards the base, but black posteriorly; the flagellum black or nearly black both below and above. Usually contrastingly pale are the clypeus and broadly the sides of the face to a level frequently about halfway between the base of the clypeus and the ocelli (but the supra-clypeal area black except sometimes at its extreme lower end). The pale coloration of the lower half of the face somewhat variable, usually faded to slightly soiled yellow, frequently semitransparent to abruptly dull on the sides of the face, the clypeus often with a dark subapical transverse band and now and then with two subparallel, short, dark, longitudinal stripes. Illustrating the range of variability in the coloration of the lower half of the face are specimens (especially those from Faro) in which the light area of the sides of the face is very dull and fades out only a little above the level of the clypeus, and the clypeus itself in such cases may be almost reddish black. All of the hairs of the head black.

THORAX: Usually black throughout, but the pronotum and the scutellum sometimes more or less invaded by reddish black. The erect hairs black throughout, even those

among the dull gray tomentum at each side of the bare middle area of the propodeum. The propodeum black to sometimes reddish black.

LEGS: Black to reddish black, including the tarsal joints, with the exception sometimes of the apical one. The hairs black, even the metatarsal brushes approximately black (although sometimes with copper reflections). However, in addition to erect black hairs, the middle trochanters below have usually dull gray tomentum and the microscopic hairs on the raised area of the under side of the hind tibiae are silvery gray.

WINGS: With the median cell, the marginal cell, and a narrow area immediately below the apical half of the marginal cell strongly smoky; the rest of the wing subhyaline. The venation deep brownish to blackish; the tegulae concolorous. The number of hamuli per lower wing is usually six, more rarely seven, very rarely five. Of 105 wings examined, 82 had six hamuli, 21 had seven hamuli, and only two had as few as five hamuli, an average of 6.16.

ABDOMEN: Deep reddish black to wholly black, with the hairs on tergites 3 to 6, as well as the hairs on the sternites, black.

MEASUREMENTS: Length 4 to 5.25 mm.; width 1.5 to 1.75 mm.; length of forewing, including tegula, 5 to 5.25 mm.

QUEEN

Unknown.

MALE

"Malar space reduced; hind tibiae with only a weak longitudinal impression; their metatarsi longer and arched" (translated from Ducke, 1916, p. 44; 1925, p. 370).

TYPE MATERIAL

Friese (1900a, p. 389) noted that his type material, consisting of four workers and one male, was from French Guiana and Peru, and that several workers were in the Brussels Museum.

DISCUSSION

This is the extreme dark form of the *tataira* complex in contrast to the light extreme represented by the form *mellicolor*, which is predominantly honey colored. In the clouding

of the light areas of the face manifested by some specimens we have a phenomenon somewhat paralleling that in *mediorufa*, in which the specimens of somewhat darker aspect have been referred by Cockerell (1917, p. 124) to *salvatoris*.

DISTRIBUTION

The variety *obscura* was described by Friese (1900a, p. 389) from French Guiana

Mann); Rurrenabaque, Río Beni, Dec. (W. M. Mann); Tumupasa, Dec. (W. M. Mann).

TRIGONA SUBGENUS SCAURA SCHWARZ

Trigona (Scaura) SCHWARZ, 1938, p. 479.

TYPE SPECIES: *Trigona latitarsis* Friese.

WORKER

DIAGNOSTIC CHARACTERS: Distinguished from the other subgenera of *Trigona* by the

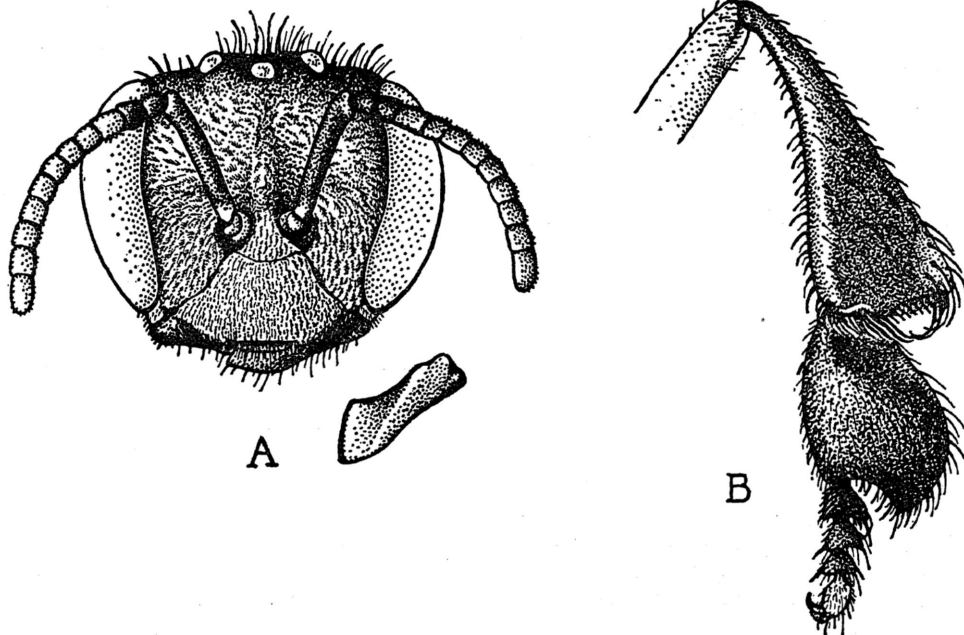


FIG. 80. Worker of *Trigona (Scaura) latitarsis* Friese. A. Head and mandible. B. Tibia and tarsal joints of hind leg. Drawings by Shirley H. Risser.

and Peru. Ducke (1916, p. 45; 1925, p. 371; 1945, p. 37) added to the range the northern part of the State of Pará, Brazil. The material before me is from the following localities:

BRITISH GUIANA: Moraballi Creek, Essequibo River, Oct. 23, 1929 (Oxford Univ. Exped.); Essequibo River at source (J. Ogilvie); between Membaru Creek and Kurupung River (upper Mazaruni District), Feb. 22, 1929 (A. S. Pinkus).

BRAZIL: State of Pará: Faro, Dec., 1905.

PERU: El Campamento, Colony of the Perené, June 19, 1920 (Cornell Univ. Exped.).

BOLIVIA: Río Negro, Jan. (W. M. Mann); Ivon, Río Beni, Feb. (W. M. Mann); Cavinass, Feb. (W. M. Mann); Huachi, Río Beni, Sept. (W. M.

following combination of characters: mandible edentate; hind metatarsus notably swollen and somewhat wider than the hind tibia; integument sculptureless or virtually sculptureless; rather triangular hind tibiae, fringed with somewhat dense, very short, simple hairs.

HEAD (FIG. 80A): Somewhat wider than the distance between the outer rims of the tegulae. Facial quadrangle moderately wide, the distance between compound eyes at the level just below the middle ocellus a little less than the distance from the middle ocellus to the apex of the clypeus. Chitin smooth. Eyes a little convergent below and each wider, when the head is viewed in profile, than the

genal area. The clypeus rather flat, barely raised, if at all, above the level of the sides of the face and about twice as wide as it is high. Its oblique sides more strongly divergent towards the apex than at the base. Its apex truncate along the middle with a fairly extensive recession at each side. The supraclypeus short, subtriangular, not prominent, barely distinguishable from the clypeus. The malar space developed slightly (*latitarsis*) to moderately (typical *longula*). The labrum simple. The mandibles (fig. 80A) overlapping, slightly hourglass shaped, their apex edentate from end to end. The ocelli arranged almost linearly, with the middle ocellus very slightly depressed and a trifle anterior to the lateral ones, which are rather strongly protruding and tilted towards the nearest compound eye. The distance between the lateral ocelli somewhat greater than that which separates each of these ocelli from the compound eye. A feeble blunt carina behind the ocelli and about coextensive with them. The lower half of the face and the genal area over most of its extent more (*latitarsis*) or less (*longula*) densely silvery gray pruinose. The upper half of the face more sparsely covered with appressed or semi-appressed silvery gray hairs and, in addition, with more erect black hairs on front and vertex. Erect hairs towards the inner part of the under side of the head. The scape more slender than the flagellum, either devoid of erect hairs (*latitarsis*) or with such hairs very fine and inconspicuous, distinctly shorter than the scape is wide (*longula*). The length of the scape about one-half that of the flagellum.

THORAX: Of smooth chitin; the greatest width of the mesonotum, at the base, barely less than the length of the mesonotum and scutellum combined. The scutellum rounded posteriorly, not in the least salient, failing to over-roof in the slightest the medianly bare and shiny propodeum. The entire thorax as well as the sides of the propodeum rather hairy; the hairs on the scutellum a little longer than those of the mesonotum.

LEGS: Progressively longer from front pair to hind pair, the long hind leg being about as extensive as the combined length of the head, thorax, and abdomen. The hind tibia (figs. 80B, 84) barely longer than the combined length of the hind femur and trochanter, its

shape subtriangular, narrow at the base, broad at the apex; the apical margin rather rounded on its anterior one-third, which bears a poorly developed comb, more emphatically rounded on the median one-third of its contour, and with a rather strong, tooth-like angle on the posterior one-third. The outer face of the hind tibiae flat towards the base, more excavated towards the apex. The inner face of the hind tibiae with a slightly raised area that is covered densely with microscopic silvery gray hairs and that contrasts with the sharply declivitous area (with longer hairs) anterior to it and the very narrow, flat, hind rim. The hind metatarsus (fig. 80B, 84) ponderous, disproportionately large and swollen, fully twice as long as the combined length of the small joints of the tarsus and slightly wider than the greatest width (along the apex) of the hind tibia. Except at the base these metatarsi are strongly swollen over their entire surface, decidedly convex along their posterior contour, narrowed somewhat towards the base, apically with a large, posterior, tooth-like angle. There are hairs on coxae, under side of trochanters, under side of fore and middle femora and outer side of hind femora (mostly silvery gray in *latitarsis*, mostly dark in *longula*); the inner side of the hind femora with silvery gray appressed hairs that are sometimes hard to detect. Hairs rather short and black on the outer and inner face of the fore tibiae but somewhat longer on the posterior margin of these tibiae; the hairs of the middle tibiae black and rather short on outer face, somewhat longer on inner face. The hind tibiae fringed anteriorly and posteriorly with notably short, rather dense black hairs, but those of the posterior fringe even shorter than those of the anterior fringe; a few such hairs also scattered over the outer face of these tibiae. The black hairs on the outer face of the fore metatarsi longer than the brushes on the inner face or than the tibial hairs. The dark hairs on the outer face of the middle and hind metatarsi subequal to, to slightly shorter than, the respective brushes on the inner face.

WINGS: With the first transverse cubital vein rather clearly demarked, the second transverse cubital as a rule only feebly indicated to obsolete. The first discoidal cell

about nine-tenths the length of the marginal. The number of hamuli per lower wing ranges from four (most exceptional) to seven (about equally exceptional), with an average around five.

ABDOMEN: At the base somewhat narrower than the thorax, arched ventrally as well as dorsally, with the segments usually exposed instead of being telescoped. Tergite 1 polished. Tergites 2 to 6 polished basally but very finely tessellated along their apex (corresponding with the presence in this area of hairs). Each of the sternites likewise with hairs along its apex.

MEASUREMENTS: Length 3.25 to 6 mm. or more; width of thorax 1.25 to 1.50 mm.; length of forewing, including tegula, 4 to 5.25 mm.

QUEEN

See descriptions of the queen under *latitarsis* and *longula*.

MALE

See descriptions of the male under *latitarsis* and *longula*.

DISCUSSION

What particularly differentiates *Scaura* from related subgenera is the very unusual thickness and width of the metatarsal joint of the hind leg of the worker, this joint being wider than the associated tibia. While the thickening of the hind metatarsus occurs in males of subgenera other than *Scaura* and the joint is apt to be a little thicker anteriorly than posteriorly even in the workers of certain species belonging to other subgenera, the ponderous hind metatarsal joint is so extreme in its development in insects like *latitarsis* and *longula* as to justify their inclusion in a distinct subgenus. In the male, too, the hind metatarsal joint is wider than the associated tibia, only slightly so in the case of *latitarsis* but, according to Ducke (1916, p. 46; 1925, p. 368; 1945, p. 38), in the proportion of 3 to 1 in *longula*. In the queen this disproportion between the two joints does not obtain.

The worker is further differentiated by the complete absence of teeth on the apical edge of the mandible, a condition which obtains also in the male and the queen of *latitarsis*

and presumably is shared also by the male and queen of *longula*.

The apex of sternite 6 (fig. 81C) of the queen of *latitarsis* is emarginate, with a resulting bidentate contour, but the teeth are not so pronounced as they are on the corresponding sternite of the queen of *Trigona* (*Cephalotrigona*) *capitata* F. Smith. Both of the specimens of the *latitarsis* queen before me are physogastric; one cannot say with certainty, therefore, whether in the virgin queen of *latitarsis* these teeth project beyond the dorsal terminus of the abdomen as they do in *capitata*. Ducke makes no mention of this sternite in his description of the queen of *longula* (1916, p. 46; 1925, p. 368; 1945, p. 38).

Most of the nests reported for this subgenus were nests located in termite structures. The more common of the two species (*latitarsis*) seems to show a rare fidelity throughout its range in South America to the nests of different species of *Nasutitermes*. At least, all the reported instances in that continent are associated with this genus of termites. The other species of *Scaura*, namely, *longula*, favors, according to Girard (1875a, p. 572), terrestrial nests of termites.

KEYS TO THE SPECIES AND VARIETIES OF *Trigona* (*Scaura*)

WORKERS

1. Relatively small, 3.25 to 4.25 mm. in length, with a wing length, including tegula, of 4 to 4.5 mm. The hairs of the mesopleura and those of the ventral surface of the abdomen silvery gray *latitarsis* Friese
Larger, 5.5 to 6.5 mm. in length, with a wing length, including tegula, of about 5.25 mm. 2
2. The mesopleura with black (sometimes dark gray) hairs. The hairs on the ventral surface of the abdomen usually black like those densely covering the apex of tergites 2 to 6 *longula* variety *longula* Lepeletier
The mesopleura with white hairs. The hairs of the abdomen white and black
. *longula* variety *tenuis* Ducke

MALES

1. The hind metatarsus only a trifle wider than the hind tibia *latitarsis* Friese
The hind metatarsus about three times as wide as the hind tibia (according to Ducke, 1916, p. 46; 1925, p. 368; 1945, p. 38)
. *longula* variety *longula* Lepeletier

Trigona (Scaura) latitarsis Friese

- Trigona latitarsis* FRIESE, 1900a, p. 388.
Melipona latitarsis, DUCKE, 1901, p. 65.
Melipona latitarsis, DUCKE, 1902a, pp. 323, 419.
Melipona (Trigona) latitarsis, DUCKE, 1902b, pp. 291, 316-317.
Trigona latitarsis, SILVESTRI, 1902a, p. 25.
Trigona latitarsis, SILVESTRI, 1902b, pp. 164-165, pl. 2, fig. 31 (identified by H. Friese).
Trigona latitarsis, SILVESTRI, 1903, pp. 187, 210.
Trigona latitarsis, BUTTEL-REEPEN, 1903a, p. 133.
Trigona latitarsis, MARIANNO, 1911, p. 114.
Trigona argyrea COCKERELL, 1912c, p. 313.
Melipona latitarsis, DUCKE, 1916, opposite p. 28, pp. 47-48.
Trigona argyrea, LUTZ AND COCKERELL, 1920, p. 495.
Trigona latitarsis, HEGH, 1922, p. 593.
Trigona argyrea, LUTZ, 1924a, pp. 207, 210, 212, 214, 220, 221 (identified by T. D. A. Cockerell).
Trigona latitarsis, LUTZ, 1924a, pp. 214, 218, 221 (identified by H. Friese).
Melipona latitarsis, DUCKE, 1925, pp. 342, 348, 366-367.
Melipona latitarsis, ALFKEN, 1930b, p. 8.
Trigona latitarsis, SCHWARZ, 1932a, p. 253.
Trigona (Scaura) latitarsis, SCHWARZ, 1938, pp. 446, 479, 480.
Melipona latitarsis, DUCKE, 1945, opposite p. 24, p. 39.
Trigona latitarsis, MICHENER, 1946, p. 195.
Trigona argyrea, COCKERELL, 1946, p. 204.

WORKER

DIAGNOSTIC CHARACTERS: Hairs of mesopleura and those of the abdomen below silvery gray.

HEAD (FIG. 80A): Black, usually with only the apical one-third of the mandible reddened and the entire scape black (specimen from Central America and from localities also in British Guiana and Brazil), but other specimens, more particularly those from Bolivia and Peru, have the mandibles more extensively ferruginous and the scape, especially below and in front, invaded in varying degrees by ferruginous. The hairs as described for the subgenus, the silvery gray appressed hairs of the lower half of the face usually dense. The erect hairs towards the inner part of the under side of the head sometimes black, sometimes silvery gray. The malar space only slightly developed, at its narrowest part only about one-half the width of the scape.

THORAX: Black, with the erect hairs of the mesonotum and scutellum black, and the erect and appressed hairs of the mesopleura and the tomentum on each side of the bare middle region of the propodeum silvery gray.

LEGS: Black to sometimes brownish, with at least the apical joint of the tarsi pale. The hairs silvery gray on coxae, trochanters, and for the most part or entirely on the femora. The hairs on the outer and inner face of the fore and middle tibiae, those fringing the hind tibiae (fig. 80B), and the hairs on the outer side of the metatarsi black. The metatarsal brushes usually very dark, black or verging on black, especially those of the middle and hind pair of legs, those on the fore pair usually more golden. The raised area on the inner face of the hind tibiae covered with microscopic, silvery gray hairs.

WINGS: Hyaline, iridescent, with the stigma and nervures fuliginous; the tegulae fuliginous to slightly fuscous. The number of hamuli per lower wing usually five, more rarely six, very rarely four, and most exceptionally seven. Of 200 wings examined, 174 had five hamuli, 22 had six hamuli, three had four hamuli, and only one had seven hamuli, an average of 5.10 per wing.

ABDOMEN: Black or more or less brown, often lighter below than above. The hairs fringing the tergites black, except that those of the apical tergite are sometimes pale. The hairs on the ventral side of the abdomen silvery gray.

MEASUREMENTS: Length 3.25 to 4.25 mm. (abdomen greatly extended); width of thorax about 1.25 mm.; length of forewing, including tegula, about 4 to 4.5 mm.

QUEEN (GRAVID)

HEAD (FIG. 81A): Relatively smaller than that of the worker, wider than the mesonotum but not so wide as the distance from the outer rim of one of the tegulae to the outer rim of the other tegula. The upper half of the head to the inclusion of the vertex with somewhat blotchy sculpturing, the lower half very finely tessellated, with a subdued sheen; the genal area somewhat more shiny. The facial quadrangle nearly as wide as the distance from the middle ocellus to the apex of the clypeus. The clypeus raised only very slightly above the level of the sides of the

face and just under twice as wide as it is high. Its oblique sides slightly more divergent towards the apex than at the base. Its apex truncate along the middle with a fairly extensive recession at each side. The supraclypeus of triangular to sugarloaf shape, rather prominent, with a fossa extending from its peak towards the middle ocellus. The malar space longer than in the worker; its length, however, hardly more than 1.5 times

lum. The head for the most part deep reddish brown, this being the prevailing color over most of the lower part of the face and over the genal area. The front and vertex largely blackish, and a spot on the malar space and the basal prominences of the mandible are black. The rest of the mandible as well as the labrum ferruginous to fulvous. The scape more or less brownish to blackish and darker than the flagellum, which tends to be mainly

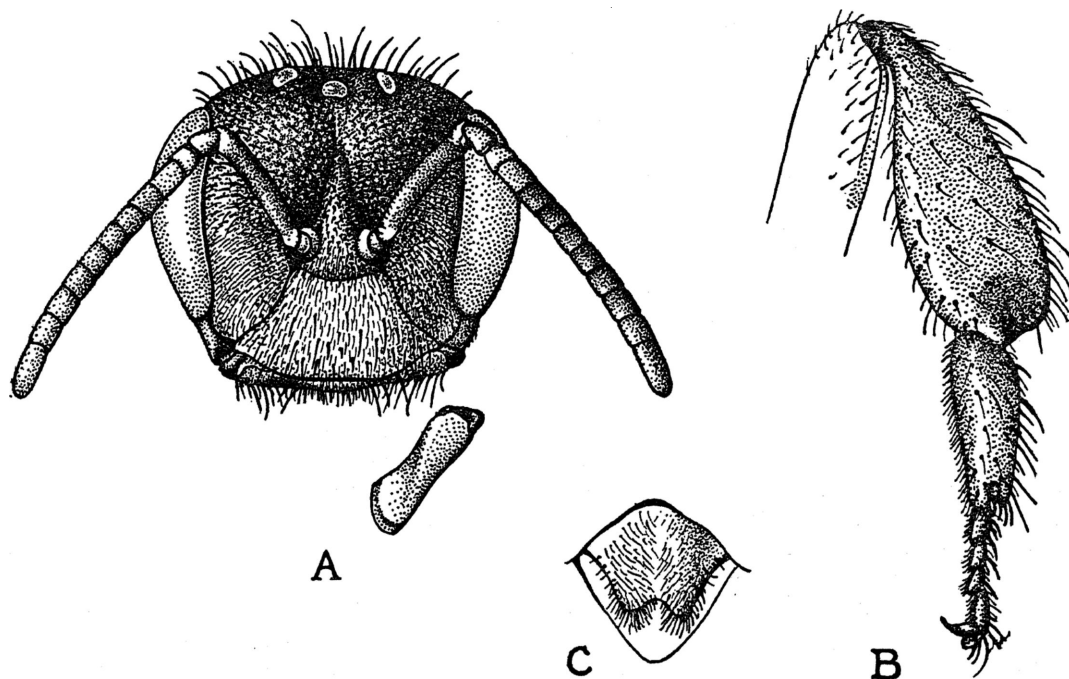


FIG. 81. Queen of *Trigona (Scaura) latitarsis* Friese. A. Head and mandible. B. Tibia and tarsal joints of hind leg. C. Sternite 6 of abdomen, seen against tergite 6 in outline. Drawings by Shirley H. Risser.

the width of the scape. The eyes almost parallel sided, short and narrow, roughly five-sixths as long as those of the worker. The labrum simple. The mandibles (fig. 81A) shaped like those of the worker, overlapping, edentate along their apical edge. The ocelli almost in a line, with the middle one in a slight depression and only slightly anterior to the somewhat outward-tilted lateral ocelli. The distance separating the lateral ocelli about equal to that which separates a lateral ocellus from the nearest compound eye. A blunt low carina behind the ocelli. The length of the scape about one-half that of the flagel-

ferruginous to fulvous, with some of the joints slightly clouded. The lower half of the face with dense, very short, plush-like hairs that are fulvous in some lights, more silvery gray in others. The hairs of the upper half of the head darker, very short on the front but abruptly longer on the vertex, being black in one of the two specimens before me but fulvous in the other. The labrum, which is shallowly emarginate along its lower margin, densely covered with fulvous hairs and the mandibles below fringed with concolorous hairs that tend to be longer than the mandible is wide. Rather long hairs, too, towards

the lower extremity of the genal area, which, however, for the most part has such inconspicuous, minute, appressed, pale hairs that at first glance they seem glabrous. The scape with no or virtually no erect hairs.

THORAX: Larger than that of the worker, for the most part smooth and shiny. The scutellum rounded posteriorly, not in the least salient, failing to over-roof in the slightest the medianly bare and rather large propodeum. The mesonotum and the scutellum more or less blackish, the mesopleura deep reddish brown, the propodeum a somewhat lighter brown. The hairs on the mesonotum and on the scutellum blackish to brownish, those of the scutellum rather long; the hairs on the mesopleura distinctly shorter and silvery gray. The short pale hairs on each side of the bare middle area of the propodeum not especially dense, with the result that these lateral areas are nearly as shiny as the hairless middle area.

LEGS: More robust than those of the worker but the hind metatarsal joint, which in the worker is so conspicuously enlarged, is in the queen barely one-half as wide as the associated tibia and not in the least swollen. The hind legs longer than the middle legs, which in turn are somewhat longer than the fore legs. The fore and middle tibiae distinctly shorter than their respective femora, reversing the condition of the hind pair of legs, in which the tibiae are longer than the femora although distinctly shorter than the combined length of the femora plus the trochanters. The hind tibiae (fig. 81B) with their anterior and posterior lateral contours convex. These tibia only a very little longer than those of the worker but rather more uniformly wide from base to apex, their width over a large part of the joint being approximately that attained by the worker only at the apex of the joint. The outer face of the joint is rather flat, particularly posteriorly. The inner face has a gently raised area covered with microscopic silvery gray hairs and very narrowly rimmed posteriorly by a sharply flattened border. The apical contour rounded anteriorly and approximately rounded posteriorly with a small and feebly protuberant rotundity between. The hind metatarsi narrow, only about one-third as wide at the base as they are long, and

narrower at the apex than they are at the base. The combined length of the small joints of the hind tarsi is about three-fourths that of the hind metatarsi. The legs for the most part light brownish, with the tarsal joints tending to be still paler. The hairs sparse, pale on the middle and fore legs, more or less brownish to blackish on the hind tibiae. The short, sparse, silvery gray hairs on the under side of the trochanters more dwarfed than the concolorous hairs of their coxae. Minute silvery gray hairs also on the basal half of the under side of the femora, which are otherwise largely to wholly glabrous (a few hairs towards the apex of the hind femora). The fore and middle tibiae glabrous or virtually so on their inner face, and the fore tibiae in one specimen also virtually glabrous on their outer face, but usually the outer face of both of these tibiae is scantily covered with a few pale, medium-sized hairs that compare in length with the pale hairs on the outer face of the corresponding metatarsal joints. The darker hairs on the hind tibiae longer and a little more abundant than the hairs on the fore and middle legs; these hairs extend over the outer face of the joint as well as along the contours, especially the posterior contour, but in no case is their length even half that of the width of the hind tibiae. The inner face of the hind tibiae densely covered with microscopic, silvery gray hairs, corresponding with the condition in the worker. The pale hairs on the outer face of the hind metatarsi scant and relatively short. The hairs of the brushes on the inner face of the metatarsi short.

WINGS: Similar to those of the worker and approximately of the same length, extending backward only to the apex of tergite 3 of the much distended abdomen. Number of hamuli in the lower wings of one of the two specimens five and six respectively, or an average of 5.5; the wings much mutilated in the second specimen and the hamuli therefore missing. The first transverse cubital vein strongly chitinized, the second feebly indicated to obsolescent.

ABDOMEN: Much distended, with the result that it is both wider and deeper than the thorax and longer than the head and thorax jointly. The first two tergites smooth and shiny, tergite 1 being glabrous and tergite 2 largely glabrous, with a few hairs for the most

part confined to its apex. The subsequent tergites finely punctate and densely and completely hairy from base to apex, the hairs being fulvous to ferruginous, of rather soft texture, a trifle coarser on the apical tergite but not in the least bristle-like. The ventral side of the abdomen with very few erect hairs along the apex of the several sternites. Sternite 6 (fig. 81C), however, densely covered with plush-like, short, erect, fulvous hairs, only the lateral expansions at the base

approximation below being about in the proportion of 4.5 to 3.25. The apico-lateral extremity of the clypeus almost grazing the rim of the compound eye. The clypeus rather flat, its height approximately two-thirds of its width; its sides oblique and barely more divergent on their lower than on their upper half; the apex truncate along its middle but recessive at each extremity. The supraclypeus short, subtriangular, not prominent, tending to merge with the clypeus. The labrum faintly

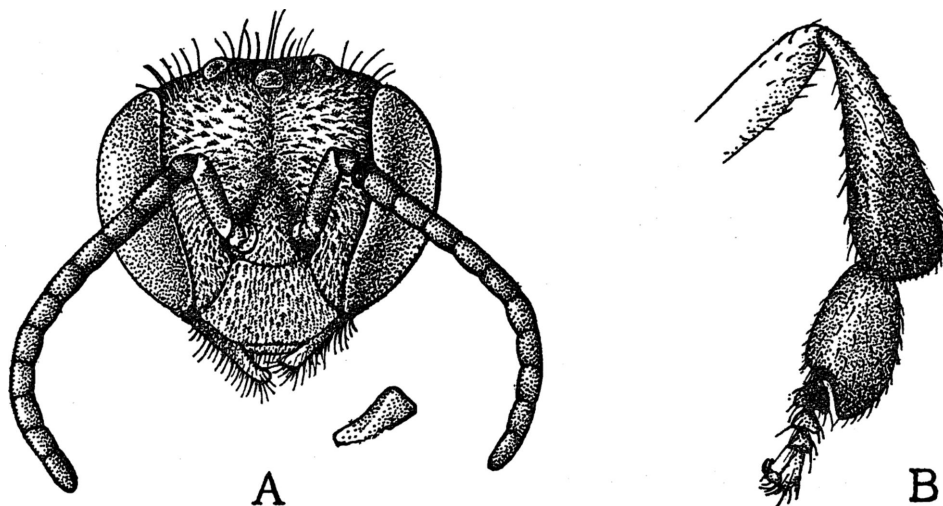


FIG. 82. Male of *Trigona (Scaura) latitarsis* Friese. A. Head and mandible. B. Tibia and tarsal joints of hind leg. Drawings by Shirley H. Risser.

of the sternite being hairless, its apex emarginate at the middle with a resulting bidentate apical contour, each of the resulting teeth being fringed densely with fine pale hairs.

MEASUREMENTS: Length about 6.5 mm. (abdomen 4 mm.); width of thorax about 1.5 mm.; length of forewing, including tegula, about 4.5 mm.

MALE

HEAD (FIG. 82A): Short compared with its width, which is greater than the distance between the outer rim of one tegula and the outer rim of the other. Chitin smooth. The eyes strongly convergent below, wider than in the worker. The facial quadrangle narrower than in the worker and much narrower below than above, the distance between the eyes near their summit and the distance separating them at their level of closest

bituberculate, suggesting the condition in *Trigona (Trigona) pallida* Latreille. The malar space reduced to the vanishing point, the base of the mandible being in contact with the rim of the eye. The mandibles (fig. 82A) when retracted, barely more than touching each other at their tips. Their apex, only about one-half as wide as their base, is edentate. The ocelli arranged almost linearly, with the middle one in a shallow depression and only slightly anterior to the lateral ones, which are raised and tilted outward. Each lateral ocellus separated from the nearest compound eye by a trifle more than its major axis. A feeble blunt carina behind the ocelli and about coextensive with them. Black or blackish, with at least the apex of the mandibles and the antennal sockets ferruginous, but in some specimens more or less ferruginous also over the base of the

mandibles, the labrum, the scape, and even the clypeus. The clypeus and at least the adjacent parts of the sides of the face, as well as the genal area over most of its extent, silvery gray pruinose. The upper half of the head somewhat less densely covered with appressed to semi-erect silvery gray hairs. The erect hairs on the vertex sometimes silvery gray but in most cases black. The erect hairs towards the inner part of the under side of the head silvery gray. The scape only about one-fifth as long as the flagellum and of about the same width; joint 3 of the flagellum, viewed from below, considerably longer than joints 1 plus 2 and, even when viewed from above, fully as long as these joints combined.

THORAX: Of smooth chitin; the combined length of the mesonotum and scutellum barely greater than the maximum width of the mesonotum at the base. The scutellum rounded posteriorly, not in the least salient, failing to over-roof in the slightest the medianly bare and shiny propodeum. Black to sometimes brownish, with the scutellum occasionally more or less ferruginous (probably callows) but more often dark. The erect hairs of the mesonotum and scutellum tend to be black, although the appressed hairs on the mesonotum (more conspicuous than the erect hairs) are silvery gray. The hairs of the mesopleura are also silvery gray. The hairs of the mesonotum fairly dense, very short, and semi-appressed to appressed; those of the scutellum distinctly longer; those of the mesopleura of intermediate length. The sides of the propodeum silvery gray tomentose, with longer concolorous hairs interspersed.

LEGS: Progressively longer from front pair to hind pair, the long hind leg being about as extensive as the combined length of the head, thorax, and abdomen. Legs predominantly smooth, finely tessellated on the inner face of the hind tibiae. The fore and middle tibia shorter in each case than the associated femur; the hind tibia longer than its femur but shorter than the femur and trochanter combined. The hind tibia (fig. 82B) clavate to subtriangular in outline, arched over most of its outer face but somewhat flattened posteriorly, especially towards the apex. The apical contour hardly more rounded anteriorly than posteriorly. The hind metatarsi more swollen than the associated tibiae and

barely wider than these, the posterior margin markedly convex, ending apically in a rather strong, tooth-like angle. The combined small joints of the hind tarsus rather shorter than the hind metatarsus. Black or blackish to sometimes extensively brownish (callows), with more particularly the apical tarsal joint and sometimes the adjoining joints pallid. Hairs short and inconspicuous, scant and silvery gray on coxae, trochanters beneath, and femora beneath or mostly beneath. The hairs of the tibiae black or mainly black but likewise very minute and inconspicuous; those towards the apex of the under side of the middle tibiae a little the longer; those over the outer face of the hind tibiae as well as along the anterior and posterior lateral contours very minute, shorter than those fringing the fore and middle tibiae. The inner face of the hind tibiae densely covered with microscopic silvery gray hairs. The brush on the inner surface of the metatarsi, particularly that of the hind metatarsi, dense but the hairs rather short.

WINGS: Hyaline, iridescent, with the stigma and nervures fuliginous; the tegulae fuliginous to slightly fuscous. Second transverse cubital vein usually only feebly indicated to absent, but the first transverse cubital more clearly traceable. The first discoidal cell nearly nine-tenths the length of the marginal. The number of hamuli per lower wing usually five, rarely six. Of 15 wings examined, 14 had five hamuli and only one had six hamuli, an average of 5.07.

ABDOMEN: At the base somewhat narrower than the thorax, elongate, with the segments usually exposed instead of being telescoped. The tergites for the most part smooth, with barely traceable sculpturing now and then along their apex, somewhat corresponding to the presence of hairs. These hairs few and for the most part minute, the appressed hairs silvery gray, the short erect hairs frequently black. The hairs negligible on tergites 2 to 4 and over most of tergite 5, but progressively longer hairs fringe the sides of tergite 5 and especially the sides of tergites 6 and 7, many of these hairs being gray. The ventral side silvery gray sericeous, more especially on sternites 3 to 5. For the structure of the sternites and genitalia, see figure 83.

MEASUREMENTS: Length about 3.75 to

4.5 mm.; width of thorax about 1.25 mm.; length of forewing, including tegula, about 4 to 4.5 mm.

TYPE MATERIAL

Friese described *latitarsis* on the basis of three workers and three males from São Paulo, Brazil, supplemented by other males from the same locality in the museum at Budapest. Among his type material were also specimens from Surinam. Cockerell's

habit of *latitarsis* is that of Silvestri (1902a, p. 25; 1902b, pp. 164-165; 1903 p. 210), who came upon only one colony of this bee at Coxipò, Brazil. It was located in a termite nest of *Nasutitermes* (*N.*) *breviocularis* that had been constructed on the trunk of a tree.¹ The entrance consisted of a wax tube, 5 cm. in length and about 10 mm. in diameter towards the base. The combs were few and small as were also the provision containers. The nest was separated from the quarters of

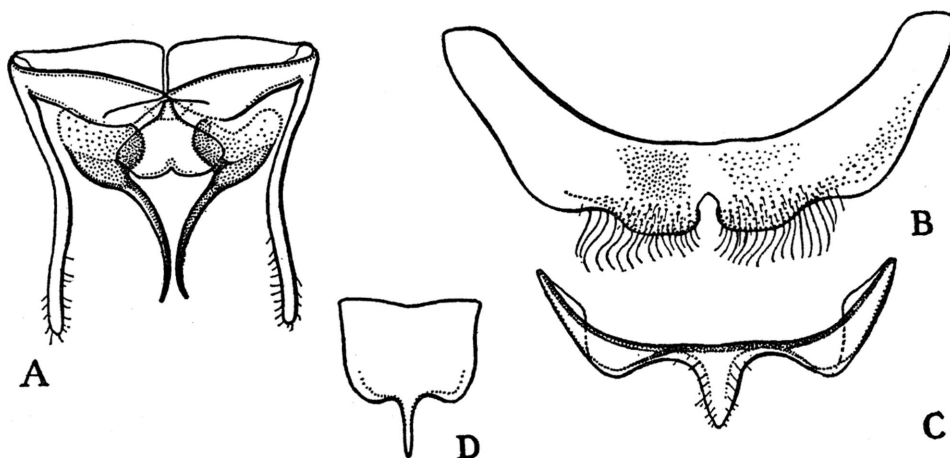


FIG. 83. Abdominal parts of male of *Trigona* (*Scaura*) *latitarsis* Friese. A. Genitalia (chitinized parts only). B. Sternite 5. C. Sternite 6. D. Sternite 7. All based on specimens from Rurrenabaque, Río Beni, Bolivia. Drawings by Shirley H. Risser.

argyrea, considered a synonym of *latitarsis*, was collected at Quiriguá, Guatemala, and is in the United States National Museum.

DISCUSSION

It has seemed preferable merely to comment on the differences noted within *latitarsis* rather than to attempt to make divisions within that species, especially as it is by no means certain that the invasions of ferruginous are not ascribable in many cases to a callow state. On the other hand, in Central American workers that are indubitably callows, the entire scape and the basal two-thirds of the mandible are black as in the fully matured adults from that region, whereas Bolivian and Peruvian specimens of much darker general appearance than these callows have the scape and mandibles more extensively ferruginous.

Possibly the first reference to the nesting

of the termite by a stratum of wax reinforced by propolis. Silvestri collected the nest, but it was subsequently ravaged by ants.

The association of *latitarsis* with termites has been confirmed by later observers. Ducke (1916, p. 48; 1925, pp. 366-367; 1945, p. 38) saw a nest of this bee from the Rio Purús, State of Amazonas, Brazil, that was located in the nest of a termite attached to the limb of a tree. The nest of the bee had a small wax entrance tube; the brood combs were horizontally arranged, one above the other, and enclosed by an involucre. From Ilha Grande in the Brazilian State of Rio de Janeiro, Dr. H. Sick has sent me various lots of *latitarsis* collected from the nests of ter-

¹ In Silvestri's records the name of the termite has been given as *Eutermis Rippertii* but, as Alfred Emerson has informed me, the reference in question should, on the basis of Holmgren's study of 1910, now read *Nasutitermes* (*N.*) *breviocularis*.

mites identified by Alfred Emerson as *Nasutitermes aquilinus* (Holmgren). These instances of a termitophile habit, reported from widely separated areas in Brazil, are supported by records also from British Guiana. There, two observers, Alfred Emerson and John Tee-Van, reported finding this bee in nests of two species of the genus *Nasutitermes*. The colony observed by Tee-Van was in a nest of *Nasutitermes* (*N.*) *ephratae* (Holmgren). The find of Emerson is described as follows: "Large nest of *Nasutitermes* (*N.*) *costalis* (Holmgren) 2.5 feet long and 2 feet wide. Surface of nest rather rough. *Trigona* nest in interior as large as a fist with many layers of brood cells and a few honey and wax cells by the side. The *Trigona* nest in the center of the termite nest. I did not see the entrance" (cited by Schwarz, 1938, p. 480).

William M. Mann while on the Mulford Biological Expedition of 1921-1922 noted a nest of *latitarsis* that was in a termite nest at Rurrenabaque, Bolivia.

Indeed the only possible exception to this termitophile habit that I have seen recorded in the literature is the brief notation regarding *argyrea* (here considered a synonym of *latitarsis*) that Cockerell reported (1912c, p. 313). It reads: "Nest in clay bank" and refers to specimens obtained by Mrs. Cockerell at Quiriguá, Guatemala. A colony of *latitarsis* was collected by G. P. Goll at Trece Aguas, Guatemala, but unfortunately the location of the nest is not indicated and therefore leaves undecided whether the above-mentioned record of Mrs. Cockerell constitutes merely an exception to the prevailing habit or is indicative of a change of behavior among the northern representatives of the species. What can be said with certainty, however, is that at least as far north as Panama association of *latitarsis* with termites still persists, for Michener (1946, p. 195) observed a nest of this bee at Cerro Campana, Panama, on August 5, 1945, that was enclosed in a termite colony about 10 feet above the ground on a small tree. It is likely, I think, that the symbiotic relationship between this bee and termites occurs throughout the range of the bee.

The nest entrance of the Cerro Campana colony of *latitarsis*, as described in a letter

received from Michener, was "tube-like, of yellow wax, soft and thin and delicate, projecting 2.75 inches from the side of the termite nest." Michener added that there was "a large sac-like pouch at the base of the entrance tube" that hung downward. There was a large swarm around this nest. On examination the individuals constituting the swarm were found to be males.

Both Silvestri and Emerson pronounced *latitarsis* unaggressive. Silvestri called it "wholly innocuous." Emerson stated, "Bees were remarkably quiet, none attempting to bite or offer defense."

This bee is reported by Ducke (1901, p. 65; 1902b, p. 317) as visiting various flowers, among them *Urena lobata*, to which it is partial, and also (1902b, p. 323) *Miconia minutiflora*.

DISTRIBUTION

The type material of *latitarsis* was obtained from São Paulo, Brazil, and from Surinam. Silvestri (1902b, pp. 164-165) reported *latitarsis* from Coxipò in the Brazilian State of Matto Grosso. Ducke (1925, p. 367) summarized its distribution as follows: "Throughout the whole Hyläa region (Amazonia as well as Guiana) not exactly rare, extends southward through central Brazil to the State of São Paulo." Ducke then listed localities in the States of Pará, Amazonas, Matto Grosso, Goyaz, and São Paulo, Brazil. The species is, however, of much wider distribution, being represented also in some of the west coast countries of South America and in Central America, as summarized in the following list:

MEXICO: State of Tabasco: Teapa, Feb. (H. H. Smith). State of Vera Cruz: Santa Lucrecia (F. Knab). State of Oaxaca: Near Rancho Monter on the Río Cajones, about 200 meters, Dec. 12, 1937, "flying around the horses" (A. Dampf).

BRITISH HONDURAS: Belize.

HONDURAS: Prieta, April 5, 1924.

GUATEMALA: State of Izabal: Quiriguá (type specimen of *argyrea*). State of Alta Vera Paz: Secanquin, Dec., 1905 (G. P. Goll); Cacao, Trece Aguas, March 21, 1907, including queen as well as workers (G. P. Goll).

COSTA RICA: Pozo Azul, June 15, 1902 (M. A. Carriker, Jr.).

PANAMA: State of Chiriqui: Bugaba, 800-1500 feet, males (Champion). Río Trinidad, March 17,

1912 (A. Busck). State of Panama: Cerro Campana, 2000 feet, swarm of males about nest, Aug. 5, 1945 (C. D. Michener).

CANAL ZONE: Barro Colorado Island, including male as well as workers (W. C. Allee).

BRITISH GUIANA: Kartabo, Aug. 7, 1920, colony in termite nest (A. Emerson), Aug. 7, 1920 (W. M. Wheeler), males collected in 1922 (J. Tee-Van); Kuyuwini River, Nov. 22, 1937 (W. G. Hassler).

PERU: El Campamento, Colony of the Perené, June 27, 1920 (Cornell Univ. Exped.); Puerto Bermudez, Río Pichis, July 12-19, 1920 (Cornell Univ. Exped.).

BOLIVIA: Santa Elena, Aug.; Huachi, Río Beni, Aug.; near mouth of Río Mapiri, Sept.; Reyes, Oct.; Rurrenabaque, Río Beni, Oct., Nov., "in termite nest," including queen and males as well as workers; Cavinás, Jan. and Feb.; Ivon, Río Beni, Feb. (All of the Bolivian specimens were collected by W. M. Mann.)

BRAZIL: State of Amazonas: Tabatinga, Oct., 1904 (A. Ducke); Vista Alegre, Rio Branco, Sept. 6, 1924. State of Pará: Itaituba, Aug. 27, 1902 (A. Ducke); Pará, Oct., 1904 (A. Ducke), Nov. 3, 1908, male (A. Ducke); Faro, Dec., 1905 (A. Ducke); Prata, June 30, 1919 (Parish). State of Mato Grosso: Coxipó, near Cuyabá, 1900; Itapura, Jan. 2, 1920 (R. G. Harris); Cicade Branco, Pôrto Velho, Aug. 20, 1943 (Mark Taylor); Karlingdale, Pôrto Velho, Sept. 3, 1943 (Mark Taylor). State of São Paulo: São Paulo, 1897, male. State of Rio de Janeiro: Ilha Grande, No. 445, June 14, 1944, No. 499, Sept. 15, 1944, No. 508, Oct. 6, 1944 (H. Sick).

Trigona (Scaura) longula variety
longula (Lepeletier)

Melipona (Tetragona) longula LEPELETIER, 1836, p. 434.

Trigona crassipes SPINOLA, 1840, p. 124.

Trigona crassipes, ERICHSON, 1841, p. 219.

Trigona longula, F. SMITH, 1854, p. 408.

Trigona crassipes, DRORY, 1874, pp. 281, 282.

Trigona crassipes, GIRARD, 1875a, p. 572.

Trigona crassipes, GIRARD, 1879, pp. 708, 725.

Trigona crassipes, TOMASCHEK, 1880, p. 63.

Trigona crassipes, SHARP, 1899, p. 65.

Trigona crassipes, FRIESE, 1900a, p. 388.

Melipona crassipes, DUCKE, 1901, p. 65.

Melipona crassipes, DUCKE, 1902a, pp. 323, 419.

Melipona (Trigona) crassipes, DUCKE, 1902b, pp. 291, 315-316.

Trigona crassipes, H. VON IHERING, 1903, p. 262.

Trigona crassipes, DUCKE, 1910b, p. 368.

Trigona crassipes, MARIANNO, 1911, pp. 88-89.

Trigona crassipes, STEP, [1915?], p. 181.

Melipona crassipes, DUCKE, 1916, p. 13, opposite p. 28, pp. 30, 45-46, pl. 2, fig. 4.

Trigona crassipes, WHEELER, 1923, p. 122.

Melipona crassipes, DUCKE, 1925, pp. 342, 349, 367-368, text fig. G, pl. 3, fig. 5.

Trigona crassipes, FRIESE, 1931, p. 9, fig. 4.

Trigona crassipes, MAIDL, 1934, p. 580.

Trigona (Scaura) crassipes, SCHWARZ, 1938, p. 479.

Melipona crassipes, DUCKE, 1945, p. 13, opposite p. 24, pp. 26, 37-39, pl. 2, fig. 4.

WORKER

DIAGNOSTIC CHARACTERS: Hairs of mesopleura black. Venter of abdomen usually with black hairs.

HEAD: Black, usually with only the apical one-third of the mandible reddened (an exception is a specimen from Pará, which has the mandibles completely ferruginous except for the sharply contrasted black basal prominences). The scape more or less ferruginous in front and usually also in back. The silvery gray appressed hairs on the lower half of the face less dense than is usually the case in *latitarsis*, the erect hairs towards the inner part of the under side of the head black; very fine minute erect hairs on the scape. The malar space at its middle somewhat shorter than the scape is wide.

THORAX: Black, with not only the erect hairs of the mesonotum and scutellum black but also those of the mesopleura, which are dense and of increasing length on the lower half of the mesopleura. The tomentum on each side of the bare middle area of the propodeum silvery gray.

LEGS: Black to sometimes brownish, with the apical joint of the tarsi pale. The hairs dark, black or blackish on the joints above the tibiae, although sometimes diluted with gray on the trochanters beneath, black on the remaining joints to the inclusion of the metatarsal joints within. The raised area on inner face of the hind tibiae and the adjacent region within of the hind femora densely covered with minute silvery gray hairs. (Fig. 84.)

WINGS: Hyaline, iridescent, with the stigma and nervures fuliginous; the tegulae appearing more fuscous owing to the presence of black hairs anteriorly. The number of hamuli per lower wing, in the 14 wings examined, were in all cases five, but probably a larger series would show variability as in *latitarsis*.

ABDOMEN: Elongated, black to deep reddish brown, with the apex of the several tergites tending to be darker than the base. The apex of tergites 2 to 6 with dense, black, rather coarse, semi-erect hairs; these hairs progressively longer and denser and the area covered by these hairs progressively greater



FIG. 84. Tibia and tarsal joints of hind leg of worker of *Trigona (Scaura) longula* (Lepeletier). Drawing by Shirley H. Risser.

from tergite to tergite, with all the exposed part of tergite 6 hairy. The venter likewise with black hairs along the apex from sternite to sternite (an exception is the specimen from Pará, which has the ventral abdominal hairs silvery gray).

MEASUREMENTS: Length 5.5 to 6 mm. (according to Friese, Marianno, and Ducke, 6 to 6.5 mm.); width of thorax 1.5 mm.; length of forewing, including tegula, about 5.25 mm.

QUEEN

"Brown; abdomen and legs lighter. Head as wide as the thorax; malar space very large. Hind tibiae and their metatarsi entirely simple, much narrower than the femur; these metatarsi measured two-thirds the length of the tibiae. Wings much shorter than in the case of the worker, in this respect recalling the condition of *Melipona scutellaris* and its relatives. The hairs of the body rust colored

to gray, on the vertex and dorsal aspect of thorax brown. Width of thorax 1.66 mm." (Translated from Ducke, 1925, p. 368.)

MALE

"Hind tibiae almost bare, arched, very narrow, only about a third as wide as their metatarsi, the latter almost as wide as in the worker but not swollen. Hair of body gray. Size that of worker." (Translated from Ducke, 1925, p. 368.)

TYPE MATERIAL

The type of *longula* is in the Muséum d'Histoire Naturelle in Paris. Lepeletier gave as the locality merely Brazil, but the label on the specimen is more specific: "Nord de la Capt. de St. Paul."

DISCUSSION

It has been customary to make *longula* a synonym of *crassipes* Fabricius, originally described as an *Apis* (Fabricius, 1793, p. 340) and later interpreted as a *Podalirius* (Latreille, 1802a, p. 379), as a *Centris* (Fabricius, 1804, p. 359; Latreille, 1809, p. 178), and as an *Anthophora* (Lamarck, 1817, p. 62; 1835, p. 281). The assignment of *crassipes* to genera of a habitus so different from that of *Trigona* should make for caution in accepting *crassipes* as one of the stingless bees. It is to be noted that Fabricius described *crassipes* from "Americae meridionalis Insulis," whereas Spinola (1840, p. 124), who is the first to interpret *crassipes* as a meliponid, had before him specimens only from Brazil, which obviously were not part of the type material of Fabricius and may well have been something other than *crassipes*. The insular representatives of *Melipona* and *Trigona* are few, and it is unlikely that a form like *longula*, relatively rare even on the continent of South America, would have an outpost in the islands. Spinola was the first to make *longula* a synonym of *crassipes*, but it is hard to believe that *longula*, which derived its name from the elongate character of its abdomen, can be the same as *crassipes*, the abdomen of which, according to Fabricius, is short ("brevis"). There is no mention in Fabricius' description of the swollen hind metatarsus, so characteristic of *longula*, although Fabricius devotes a fair proportion of

his brief description to the hind legs. For these reasons I reject the conclusion that *crassipes* and *longula* are the same insect and even think it very unlikely that *crassipes* is a *Trigona*. The name *longula* is here restored as the oldest existing name for the bee we are discussing, although Lepeletier's brief description might be applied to other *Trigona* with equal propriety, and I am not completely convinced that the specimen I saw in Paris that bears the type label is indeed the valid type. However, it seems wiser to accept it as the type rather than invoke further controversy.

The description of the worker of *longula* here offered is based on the few specimens before me, supplemented by notes I made on the alleged type in Paris. It is to be noted that whereas all of these specimens and the type have black hairs on the mesopleura, in contrast to the condition in *latitarsis*, Friese (1900a, p. 388) spoke of the thoracic hairs other than the black hairs on the mesonotum as fuliginous, and Ducke (1902b, p. 316) designated the thoracic hairs other than these black hairs of the mesonotum as gray and later (1925, p. 367) as more or less dark gray. Likewise Marianno (1911, p. 88) alluded to the thoracic hairs other than those of the mesonotum as gray. It may be, therefore, that there are gradations from the uniform black of the type specimen and the specimens of *longula* before me through dark gray to finally white in what Ducke (1916, p. 46) described as the variety *tenuis*. The specimen from Pará alluded to in the above description tends in this direction. Ducke also emphasized the more reduced size of the malar space as characteristic of *tenuis*.

As for the malar space, that of the specimens of *longula* before me is a little longer than the very brief malar space of *latitarsis* but hardly more than one would expect in proportion to the greater size of *longula*. Indeed these two insects are, except for their size, extraordinarily alike, and I should be tempted to regard them as merely varieties the one of the other rather than distinct species, if it were not for the doubts raised by the male. I have not available, unfortunately, a specimen of the male of *longula*, but Ducke (1916, p. 46; 1925, p. 368; 1945, p. 38) indicated that the hind metatarsus is strikingly

wider compared with the tibia in *longula* than it is in *latitarsis*.

Ducke was fortunate in locating a nest of this species, which he describes (1925, p. 368) as follows: "Once observed by me near Belem, in a hollow limb of a tree. Outer structure of wax, in the form of a long thin tube; brood-cells arranged in combs, involucre present. Honey sweet, but with an unpleasant taste of herbs. Bees timid."

On the other hand, Girard reported (1875a, p. 572; 1879, p. 725) this bee under the name of *crassipes* as nesting in the hollow of a termite nest, "living pacifically in the midst of the termites," which are described as being of the size of the European *Termes lucifugus* Rossi. Girard indicated, furthermore, that the termite structures favored by the bee are subterranean and in earth packed about the roots of a tree. Wheeler (1923, p. 122) also referred to this bee as one of the species that "build in the center of termite nests." Such a termitophile habit is in accord with what has been reported as almost exclusively the propensity of the closely related *latitarsis* and makes one wonder whether, in spite of the observation of Ducke, *longula*, too, does not favor preponderantly a termite structure for the foundation of its nest. This indeed was the conclusion of Drory (1874, p. 282), who had come into possession of two nests of this bee, which he refers to under the name of *Trigona crassipes*, both located in a termite colony. Drory indicated that the nest structure of the termite and that of the bee were located between the roots of a tree. Probably both Drory and Girard were referring to the same nest material.

Ducke (1901, p. 65; 1902b, p. 316) noted that among the flowers visited by this species are Piperaceae and also (1902a, p. 323) *Miconia minutiflora*, a member of the Melastomaceae.

DISTRIBUTION

This insect was described merely as from Brazil, whereas the designated type, as already indicated, came from the north of the "Capitainerie de St. Paul." Marianno (1911, p. 89) recorded it from Bahia and Pará, and Ducke (1916, p. 46; 1925, p. 368; 1945, p. 38) listed various places in the latter state where *longula* had been collected.

The specimens before me are few but they indicate a rather wide distribution of this species:

BRAZIL: State of Pará: Pará, March, 1901 (A. Ducke).

BOLIVIA: Cavinás, Jan. (W. M. Mann); Ivon, Río Beni, Feb. (W. M. Mann).

PERU: Puerto Yessup, Río Aguachini, July 11, 1920 (Cornell Univ. Exped.); Puerto Bermudez, Río Pichis, July 13-19, 1920 (Cornell Univ. Exped.); La Sombra to El Encanto, Putumayo District, Aug. 23, 1920 (Cornell Univ. Exped.); middle Río Ucayali, Oct. 27, 1923 (H. Bassler).

Trigona (Scaura) longula variety
tenuis (Ducke)

Melipona crassipes variety *tenuis* DUCKE, 1916, pp. 46-47.

Melipona crassipes variety *tenuis*, DUCKE, 1925, p. 368.

Melipona crassipes variety *tenuis*, DUCKE, 1945, p. 38.

WORKER

"Malar space very small. Abdomen very thin. Hairs of the sides of the thorax white, those of the abdomen white and black." (Translated from Ducke, 1916, p. 46; 1925, p. 368; 1945, p. 38.)

QUEEN

Unknown.

MALE

Unknown.

TYPE MATERIAL

Presumably the type material is in the Museu Paraense, Pará, Brazil.

DISCUSSION

See discussion of *longula* variety *longula*.

DISTRIBUTION

Ducke gave the range of this variety as: "westerly and south central parts of Amazonia," the locality records being as follows:

BRAZIL: State of Pará: Itaituba, on the lower Tapajóz. State of Amazonas: Rio Javary and Rio Japurá. State of Matto Grosso: Upper Tapajóz region.

TRIGONA SUBGENUS MOURELLA SCHWARZ

Trigona (Mourella) SCHWARZ, in Moure, 1946a, pp. 442-443.

TYPE SPECIES: *Melipona caerulea* Friese.

WORKER

DIAGNOSTIC CHARACTERS: Head and thorax metallic blue. Tessellated on head, thorax, over most of middle as well as sides of propodeum, and on apical half of the several abdominal tergites. Mandible with two small teeth towards inner end of apical margin. Facial maculations sparse and confined to lower half of head. Pronotum, mesonotum, axillae, and scutellum banded, the mesonotum often only feebly. Scutellum extended only barely beyond extreme base of propodeum. Middle of propodeum with some hairs but these less abundant than hairs of the sides. Contour of hind tibiae elongately triangular with a distinct angulation at the apex posteriorly. Stigma narrow but relatively wider than in *Melipona*, and not emarginate below. Six to eight hamuli per lower wing. Hairs abundant over entire body, on lower half of head as well as upper, many of the hairs being branched or incipiently branched.

The present subgenus is monotypical, and the reader is referred to the description of the species and to the discussion for further details.

Trigona (Mourella) caerulea (Friese)

Melipona caerulea FRIESE, 1900a, p. 394.

Trigona cyanescens FRIESE, 1911, pp. 455-456.

Melipona caerulea, DUCKE, 1916, opposite p. 28, pp. 36-37, 142-143.

Trigona caerulea, BERTONI, 1918, p. 224.

Melipona caerulea, DUCKE, 1925, pp. 343, 353, 408.

Melipona caerulea, GUENTHER, 1931, p. 376.

Trigona caerulea, SCHWARZ, 1932a, pp. 257, 258-259.

Melipona caerulea, DUCKE, 1945, opposite p. 24, pp. 30, 107-108.

WORKER

HEAD (FIG. 85): Dark metallic blue, with a transverse subapical pale yellow stripe on the clypeus that is slightly emarginate usually at the middle above and frequently flanked by a small, more or less crescentic spot in each of the lower corners of the sides of the face. Usually two small upwardly convergent stripes (that fail, however, to unite) on the supraclypeus or mere vestiges of these stripes. The labrum yellowish to ferruginous as are the mandibles over their

basal half, more deeply reddish towards the apex, with the basal prominences black. The head wider than long, extending to each side somewhat beyond the outer rim of the tegulae. The facial quadrangle wide, the distance between the compound eyes at the level just below the anterior ocellus about equal to the distance from the anterior ocellus to the apex of the clypeus. The compound eyes rather strongly convergent below, the distance that separates them at their level of greatest approximation (below) being about

extremity of the eye to the base of the mandible at the middle less than the width of the flagellum. The labrum simple. The supraclypeus no more prominent than the clypeus, subtriangular in contour, longer than wide, its summit connected with the middle ocellus by a shallow fossa. The middle ocellus barely anterior to the lateral ocelli, slightly depressed. The lateral ocelli slightly tilted each towards the nearest compound eye. The distance between the lateral ocelli slightly exceeding that which separates

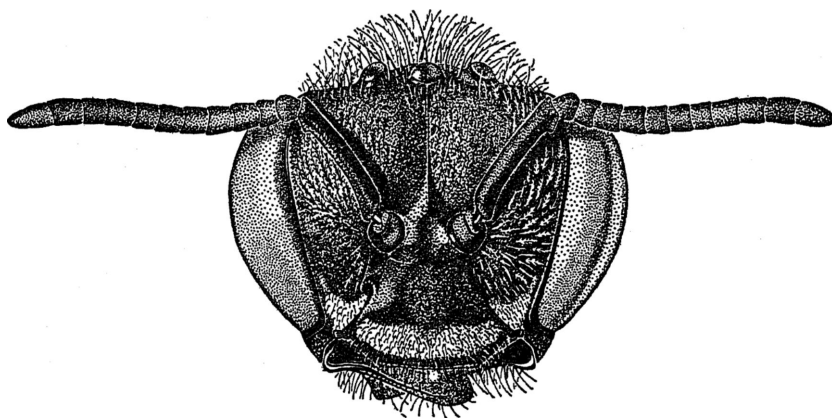


FIG. 85. Head of worker of *Trigona (Mourella) caerulea* Friese.
Drawing by Alice Gray.

as 4 is to 5 when compared with their divergence at the level just below the anterior ocellus. The clypeus raised only slightly above the sides of the face, very gently arched, not foveate apically. The length of the clypeus fully two-thirds its greatest width measured from one anterolateral extremity to the other. The sides of the clypeus oblique, being evenly slanted without abrupt divergence to their level of greatest separation below; the apex widely truncate along the middle with a slight recession towards each of its ends; the apico-lateral extremities of the clypeus approximate a rectangle and are separated each from the nearest compound eye by about the width of the flagellum. The mandibles (fig. 86) overlapping, widest at the base and apex, narrowed towards the middle; their apex edentate along the outer one-half to two-thirds but with two small denticles on the inner one-third. The malar space measured from the lower

each lateral ocellus from the nearest compound eye. The head finely tessellated. The hairs erect and silvery gray, many of them plumose, short over the clypeus, sides of face,



FIG. 86. Mandible of worker of *Trigona (Mourella) caerulea* Friese. Drawing by Alice Gray.

and labrum, longer over the front, attaining their maximum length on the vertex, also rather long over the genal area and fringing the mandible below. The antennal sockets ferruginous. The scape usually entirely black; the flagellum black above, usually more or less dull brownish below, about twice as long as the scape.

THORAX: Dark metallic blue, with the fol-

lowing areas yellow: a transverse stripe, interrupted at the middle, across the pronotum; the tubercles; a narrow stripe often very faint or absent along the sides of the mesonotum from the middle of the tegulae to the axillae, which are much more strongly maculated, with an equally strong maculation extending thence in a half circumference around the posterior border of the scutellum. The thorax above and on the



FIG. 87. Tibia and tarsal joints of hind leg of worker of *Trigona* (*Mourella*) *caerulea* Friese. Drawing by Alice Gray.

sides as well as over most of the propodeum finely tessellated (a little more coarsely so over the sculptured part of the propodeum); the V-shaped area on the declivitous part of the propodeum is, however, prevaillingly smooth and shiny. The mesonotum exclusive of the scutellum slightly wider at the base than it is long, about in the proportion of 5 to 4. The scutellum short, about twice as wide as long, rounded behind with usually a very feeble nick at its posterior middle, only barely extended over extreme base of the propodeum. The hairs erect and silvery gray, moderately dense but nowhere concealing the surface, fairly uniform in length, without strong contrast between the hairs of the mesonotum and those of the scutellum.

LEGS: Reddish brown to blackish, without or virtually without trace of metallic sheen; all the tibiae with a small pale yellow spot (sometimes indistinct) at the base of their outer face, the maculation being largest on

the hind tibiae. Legs progressively longer from the fore pair to the hind pair. The tibiae of the fore legs shorter than their femora; those of the middle legs a little shorter than their femora; those of the hind legs longer than their femora but somewhat shorter than their femora plus their trochanters. The contour of the hind tibiae (fig. 87) elongately triangular; their anterior lateral contour straight; their posterior lateral contour convex; their apex with an inconspicuous angle anteriorly that bears the comb, followed by a curvilinear bulge in the contour that is in turn succeeded by a distinct angulation posteriorly; their outer face gently arched over the basal two-thirds but concave posteriorly over the apical one-third. The inner face of the hind tibiae unevenly gabled, the backward-sloping and longer plane without a distinct posterior rim. The hind metatarsi at their widest a little more than one-half the width of their tibiae, their posterior contour convex, narrowed towards the base, the posterior angle of the apex somewhat acute and slightly down-pointing. The tessellated parts of the legs with somewhat more dainty tessellation than that on the mesopleura. The tessellation densest on the outer face of the fore and middle tibiae and the inner face of the hind tibiae. Coarser and more scattered punctation here and there on the other joints; the outer face of the hind tibiae predominantly smooth and shiny, especially on the apical one-third posteriorly. The hairs of the leg throughout silvery gray except those of the metatarsal brushes, which are light golden. The hind coxae with longer hairs than the fore and middle coxae; the trochanters all with fringes of hair below, which are continued on the under side of the femora; the fringes of the under side of the fore and middle femora have much longer hairs (particularly near the base of the joint) than are present on the upper side of the middle femora; the upper side of the fore femora largely lacks hairs. In the hind femora the situation is reversed, the hairs on the upper side of the joint being longer than those of the under side. The hairs on the outer side of the fore and middle tibiae short and dense, dwarfed by the longer hairs that fringe these joints posteriorly and by the hairs on the under side of the middle tibiae,

which increase in length towards the apex of that joint. The hairs fringing the anterior lateral contour of the hind tibiae (especially those near the apex of the joint) notably longer than the hairs of the denser fringe along the posterior lateral contour of the joint. The inner face of the hind tibiae densely covered with microscopic hairs. Hairs on the outer face of the fore, middle, and hind metatarsi and those fringing the fore metatarsi posteriorly longer than the hairs of the corresponding metatarsal brush.

WINGS: With the first discoidal cell about four-fifths as long as the marginal. The marginal cell closed or virtually closed, with only a brief weakening of the marginal vein at its apical extremity. The stigma small but complete. The first transverse cubital vein obsolescent, the second barely traceable. The number of hamuli per lower wing ranged, in the 14 wings available for study, from six to eight, with an average of 7.14.

ABDOMEN: Blackish, with here and there barely a feeble metallic reflection; usually telescoped, of comparable width to the thorax. Tergite 1 with its basal depression polished and the basal region of its dorsal face also without sculpturing, but the apex of this dorsal face usually with some feeble tessellation. The tessellation stronger on the apical half (usually all that shows in the telescoped abdomen) of the subsequent tergites, but the concealed basal part, when exposed, proves to be sculptureless or nearly so. Microscopic silvery gray hairs rather densely present over the tessellated apices of the tergites, those on tergites 4, 5, and 6 barely less stunted than those on the basal tergites. The exposed apical part of the sternites likewise tessellated and covered rather densely with silvery gray hairs that, while short, are at least in the middle region of the successive sternites distinctly longer than the hairs of the tergites.

MEASUREMENTS: Length 4.75 to 5.75 mm.; width of thorax 1.75 to 2 mm.; length of forewing, including tegula, about 5 to 5.25 mm.

QUEEN

Unknown.

MALE

Unknown.

TYPE MATERIAL

This species was erected on the basis of a single worker collected at Blumenau, Brazil.

DISCUSSION

The present species is unique among the known New World Meliponidae in being metallic colored. It was originally described by Friese (1900a, p. 394) as a *Melipona* and subsequently (1911, pp. 455-456) under a different specific name (*cyanescens*) as a *Trigona*. The two distinct generic assignments made at different times by the same investigator indicate the difficulty in placing this bee with confidence. In some ways it seems a dwarf-like member of *Melipona*, with similar hind tibiae and with hairs over the middle region of its propodeum, a character shared by few stingless bees other than *Melipona*. However, it is probably even closer to *Trigona* subgenus *Plebeia*. Its stigma is fuller than in species of *Melipona*; its propodeum less densely sculptured; the hair of its mesonotum is relatively sparse, and its size more nearly accords with the larger species belonging to the subgenus *Plebeia* than it does with the much larger *Melipona*. Ducke (1925, p. 353) placed *caerulea* between his Group IV, which included such subgenera of *Trigona* as *Plebeia*, *Paratrigona*, and *Nanotrigona*, and his Group VI, confined to *Melipona*.

Nothing is as yet known of the biology of *caerulea*. A knowledge of its biology might aid in interpreting its systematic position.

According to Guenther (1931, p. 376) the popular name of this bee is "mandaguary," a designation which Ducke (1925, p. 343) applies to *Trigona* (*Scaptotrigona*) *postica* Latreille.

DISTRIBUTION

Ducke (1925, p. 408) called attention to the fact that *caerulea* is restricted to the moist eastern part of the southern subtropical area, having been reported from Indayal in the Brazilian State of Santa Catharina, from São Lourenço in Rio Grande do Sul, and from certain localities in Paraguay.

To these records the material before me adds another country:

ARGENTINA: State of Misiones: Posadas, June 15-24, 1920 (Cornell Univ. Exped.).

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1. References devoted to New World stingless bees
2. References devoted to Old World stingless bees
3. References devoted to both New World and Old World stingless bees, or those that are general in character

The attempt has been made in the Bibliography to include as many works as possible bearing on the stingless bees, their biology, and their products, whether these works are cited in the text or not, and to exclude works that do not deal with stingless bees even though for purposes of comparison citation is sometimes made from such works in the text. Where such extraneous citations occur, the bibliographical reference has been given in full in the context.

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